

PROCEEDINGS

OF THE

SEVENTH INTERNATIONAL BOTANICAL CONGRESS

STOCKHOLM JULY 12-20 1950

Edited for the Executive Committee by

HUGO OSVALD and EWERT ÅBERG



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THE VIGNETTE displayed on the title page originates from
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Uppsala, for his expert advice in this matter.

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III. CARL MALMSTRÖM; A. NYGREN and EWERT ÅBERG; the Organizing Committee.	
IV. The Opening Ceremony.	
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XX. Pictures from some of the excursions.	

EDITOR'S PREFACE

In the spring of 1950, some months before the Seventh International Botanical Congress, the Organizing Committee discussed the question of how to edit and publish the proceedings of the Congress. The arrangement first envisaged could unfortunately not be realized, and therefore it was decided that each recorder should answer for his own section, and the Secretary General for the general part of the proceedings, the Plenary Sessions, General Meetings, etc. In addition, a chief editor was to be appointed to act as coordinator and to keep contact with the printer. At a meeting on May 19, 1950, the present editor was appointed.

In the autumn of the same year the editorial work was able to begin. The recorders started collecting the papers and the contributions to the discussions; they arranged the material according to the individual sessions where it had originated, and revised the manuscripts from a scientific and linguistic point of view. As a result, the editor's main task was to try to attain the greatest possible uniformity in the arrangement of the material and typographical treatment. In addition, it proved necessary to have a considerable amount of further linguistic revision done through the editor's office.

Since the number of papers read at the Congress was very large, the Organizing Committee had decided that only the addresses at the Plenary Meetings and the lectures at the General Meetings should be published in full, while the papers read at the sectional meetings were to be published as abstracts. On the other hand, it was not considered appropriate to lay down any hard and fast rules for the length of the abstracts, and this accounts for their varying length: Some of the sectional papers have actually been included almost in full.

One section alone has been treated in a different way—the Nomenclature Section. No papers were read here, but the sessions were devoted exclusively

to discussions of proposals that had been collected and published before the Congress by the International Commission of Taxonomy of the IUBS. The Nomenclature Section requested that the minutes from the sessions be published in full, and the Organizing Committee endorsed this request.

The editor was initially inclined to publish the proceedings in two volumes. For many reasons, however, it proved more convenient to have proceedings of this kind in one volume, and by choosing a rather large size the proceedings could be published in the way in which they are now presented. Needless to say, it has been the editor's aim to try to attain the greatest possible typographical uniformity. However, as the work progressed it was realized that it was practically impossible to maintain complete consistency in such matters as spelling and the like. With regard to English—the language employed by the majority of the authors—it has thus been necessary to allow different spellings of such words as "realize", "colour", etc. Further, some inconsistencies were inevitable with regard to the use of *italics* and CAPITALS, if only on account of the varying usages in different countries. The editor is hopeful that these inconsistencies will not seriously tax the reader's patience.

It may be mentioned here that all addresses, titles, etc. refer to the situation in 1950. For instance, the Patron of the Congress, the present King of Sweden, is referred to as H.R.H. the Crown Prince of Sweden.

Over three years have now elapsed since the Congress convened, and the editor is fully aware of the fact that botanists all over the world have been impatient at the rather long time they have had to wait for these proceedings. He must refer to the considerable size of this volume as one of the causes for the long delay. There is, however, another and more important reason. The editorial work was

Editor's Preface

certainly able to be begun in the autumn of 1950, when different schemes for the typographical form of the proceedings were considered and directions were given to the recorders. But it took a long time to collect the material in its entirety. Some of the recorders were able to deliver complete manuscripts during the spring and summer of 1951. Other recorders met with greater difficulties. In fact, the last manuscripts were not received until the end of 1952. Among these late contributions there were also some for the general part of this volume. As a result, the final revision of the proofs, pagination, and similar work could not be undertaken until sometime in the spring of this year. Nor were, unfortunately, the editors in a position to devote all their time to the Congress Proceedings.

There have been suggestions that it would have been better to omit contributions which had not reached the recorders or the editor by a certain deadline. If this had been done, it might have been possible to publish the proceedings one year earlier. Such a procedure was in fact considered, but after discussing the issue with several people the editor arrived at the conclusion that the result of such a drastic step would have been that essential parts of the proceedings would have had to be omitted, and it was felt that the advantage of having the volume published, say, in 1952 (or in the beginning of 1953) was not great enough to warrant such a procedure. The editor is convinced that most readers, let alone those in the future, will appreciate having the Congress Proceedings complete with the printing year of 1953 instead of having them badly mutilated, and printed, in 1952. That, at all events, is how those in the editor's office looked upon the situation and the editor would only add that we hope that those holding another view will forgive us now that this volume, though late, has appeared.

When this work was ready to go to press, the cost of printing was certain to exceed the funds available for the purpose, the reason being an appreciable rise in production costs in 1951-52. Additional funds had to be raised, and thanks to the generosity shown by the Swedish Government and

some private persons and companies our efforts were successful. In this connection most sincere thanks are due to the Minister of Education, Mr. Ivar Persson.

From the above it may readily be seen that the editing of these proceedings required close cooperation between the recorders and the editor's office. On this occasion, it is a pleasant duty for the editor to express to all those engaged in the editing of this work his heart-felt thanks for what has been a most agreeable collaboration. First and foremost, he is indebted to his closest collaborator, the General Secretary of the Congress, Dr. Ewert Åberg, who has taken charge of most of the extensive correspondence required for the editorial work.

The editor also wishes to express his sincere thanks to the Printer, *Almqvist & Wiksell* at Uppsala, for the great interest they have taken not only in the Proceedings but in all the other publications of the Congress. These thanks are directed in the first place to various members of the staff, Mr. O. Svensson, who designed the layout of this volume and the arrangement of the plates, and to Mr. G. Nyström, who had this book under his guidance, as well as to Dr. W. N. Lansburgh, who in a very meritorious way assisted in the linguistic revision of the proofs, and who has also revised the final proofs both from a linguistic and a typographical point of view. Finally, grateful acknowledgements are due to the managing director of *Almqvist & Wiksell*, Mr. G. Z. Hægström, for the valuable support he has given by taking over the financial risk for the 750 copies of the Proceedings which are available for sale.

And lastly, please allow the editor to express the sincere hope that these Proceedings may recall to the memory of all Congress members those pleasant and interesting days passed in Stockholm and elsewhere in Sweden in the summer of 1950, and, above all, a magnificent scientific achievement by botanists from very nearly the whole world.

HUGO OSVÄLD

Uppsala, December 1953.

PATRON

H.R.H. THE CROWN PRINCE

OF SWEDEN

INCEPTION OF THE CONGRESS

At the Opening Plenary Meeting of the Sixth International Botanical Congress in Amsterdam, 1935, Prof. N. E. SVEDELIUS, in the name of the Swedish Government, invited the meeting to hold the next Congress in Sweden in 1940. The invitation was supported by Prof. ROB. E. FRIES, and at the Final Plenary Meeting of the Congress it was unanimously accepted.

A meeting of Swedish botanists was therefore arranged in Stockholm on the 19th of October 1935 to discuss arrangements for the Seventh International Botanical Congress. At the meeting it was decided that the Congress should be held in Stockholm. An Organizing Committee was formed and Prof. ROB. E. FRIES was elected Chairman of the Committee and also President of the Congress. Prof. N. E. SVEDELIUS was elected Vice President, Dr. RUDOLF FLORIN, Secretary-General, and Dr. O. HEILBORN, Treasurer. This Organizing Committee made arrangements for the Congress to be held at Stockholms Högskola, July 17-25, 1940 and also arranged for excursions before, during and after the Congress. The outbreak of World War II in 1939, however, forced the Committee to give up the plans for holding the Congress in 1940, and at a meeting on September 19, 1939, it was decided to postpone it until after the war.

During the planning of the Congress all the officers remained in office with the exception of Dr. RUDOLF FLORIN who resigned on December 20, 1938 and was replaced as Secretary-General by Prof. HUGO OSVALD. After the end of the war in 1945 plans were again made for having the Congress in Stockholm. On October 10, 1946 another meeting of Swedish botanists was called and it was decided that the Congress be held in Stockholm in 1950. Prof. ROB. E. FRIES expressed his desire to resign as

Chairman of the Organizing Committee and President of the Congress. Prof. C. SKOTTSBERG was elected in his place. Prof. FRIES was elected Honorary Chairman. Prof. OSVALD remained as Secretary-General, Dr. EWERT ÅBERG was elected Assistant Secretary-General and Prof. CARL MALMSTRÖM became Treasurer in place of Dr. O. HEILBORN, who died in 1943. On May 18, 1948, Prof. OSVALD was elected Vice Chairman of the Organizing Committee and one of the Vice Presidents of the Congress. Dr. ÅBERG succeeded him as Secretary-General and Dr. AXEL NYGREN was elected Assistant Secretary-General.

An Honorary Committee of men representing Sweden's public and scientific life was appointed and a number of prominent foreign botanists were elected Honorary Presidents.

A Congress Bureau with Mrs. KARIN PRAVITZ in charge was organized and a Ladies' Committee was formed with a view to entertaining all those who accompanied the active members of the Congress. Dr. H. VIRGIN was put in charge of exhibits during the Congress and Mr. M. RYBERG was made responsible for relations with the press.

The Congress was organized on fifteen sections: Agronomic Botany, Cytology, Experimental Ecology, Experimental Taxonomy, Forest Botany, Genetics, Morphology and Anatomy, Mycology and Bacteriology, Nomenclature, Paleobotany, Phytogeography (with Comparative Ecology), Phytopathology, Plant Physiology, Taxonomy: Cryptogams, and Taxonomy: Phanerogams. Besides these sections a Palynological Conference was arranged.

Twenty-three excursions were arranged for Congress members, all being organized by specialists. Of the excursions 7 were made before,

6 during and 10 after the Stockholm meetings. Before the Congress the excursions were arranged in south and middle Sweden, during the Congress week in the Stockholm Archipelago and Uppsala, and after the Congress in the northern parts of Sweden.

In April 1947 a first notice (Communication No. 1) about the Congress was mailed to botanists the world over. A preliminary outline of the program and of the excursions (Communication No. 2) was mailed in April 1949 and further information (Communication No. 3) was sent in October 1949. The general program, list of members etc. were included in Communication No. 4, which was distributed at Congress Headquarters at the time of registration. At that time also a copy of "A Short History of Botany in Sweden" by ROB. E. FRIES et al. was given to each congress member. All these publications were printed in English. Before the Congress meetings those who wanted to read a paper were asked to submit an abstract, and these abstracts were mimeographed and distributed during the sessions.

As the Congress was the first one for fifteen

years the number of participants was expected to be larger than at earlier Congresses. That this was so can be seen from the following list of the number of participants in the seven International Botanical Congresses held since 1900.

Paris 1900: 233 members (169 from France, 64 foreigners).

Vienna 1905: 504 members (282 from Austria and Hungary, 222 foreigners).

Brussels 1910: 305 members (75 from Belgium, 230 foreigners).

Ithaca, N. Y. 1926: 912 members (819 from U. S. A. and Canada, 93 foreigners).

Cambridge 1930: 1175 members (487 from Great Britain, 688 foreigners).

Amsterdam 1935: 963 members (252 from the Netherlands, 711 foreigners).

Stockholm 1950: 1521 members (278 from Sweden, 1243 foreigners).

At the Congress 54 countries were represented. Among these 21 were European, 10 African, 8 Asiatic, 10 South and Central American and 3 North American. Australia and New Zealand were also represented.

THE CONGRESS ORGANIZATION

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VICE PRESIDENTS

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DR. EWERT ÅBERG

ASSISTANT SECRETARY GENERAL

DR. AXEL NYGREN

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Professor G. EINAR DU RIETZ, Växtbiologiska Institutionen, Uppsala 8
Professor G. EDMAN, Avdelningen för Botanik och Farmakognosi, Kungl. Farmaceutiska
Institutet, Stockholm
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Professor R. FLORIN, Bergianska Trädgården, Stockholm 50
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Professor T. LAGERBERG, Ringen 69, Mörby, Stocksund
Professor TH. LINDFORS, Statens Växtskyddsanstalt, Stockholm, 19
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Professor G. SUNDELIN, Statens Jordbruksförsök, Uppsala 7
Professor N. E. SVEDELIUS, Kyrkogårdsgatan 5 A, Uppsala
Professor N. SYLVÉN, Vegagatan 16, Lund
Professor SVEN THUNMARK, Linnéologiska Institutionen, Lund
Professor G. TURESSON, Botanisk-Genetiska Institutionen, Uppsala 7
Professor HENNING WEIMARCK, Botaniska Museet, Lund
Dr. EWERT ÅBERG, Institutionen för Växtodlingslära, Uppsala 7 (Secretary General)
Professor Å. ÅKERMAN, Sveriges Utsädesförening, Svalöf

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Professor KARL BJÖRLING, Institutionen för Växtsjukdomslära, Uppsala 7 (PHP)
Professor H. LUNDEGÅRDE, Växtpysiologiska Institutionen, Uppsala 7 (PHYS)
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Dr. GUNNAR ERDTMAN, Palynologiska Laboratoriet, Nyångsvägen 152-154, Bromma

CONGRESS BUREAU

Mrs. KARIN PRAVITZ, in charge

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Fil. lic. MÅNS RYBERG

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Professor S. N. WINOGRADSKY, France
Professor W. ZIMMERMANN, Germany
Dr. R. ZON, U. S. A.

SUMMARY OF THE PROGRAM

- | | | | |
|-------------|--|------------|---|
| July 7-11. | Meetings of the Section of Nomenclature.
Meetings of the Botanical Section of the International Union of Biological Sciences. | 11.30 a.m. | Visit to the Forest Research Institute, the National History Museum and the Bergius Botanic Garden. |
| July 10-11. | Palynological Conference. | July 16. | 9 a.m. Excursion to Uppsala. |
| July 12. | 10 a.m. First Plenary Session.
1 p.m. Sectional Meetings.
5 p.m. Visit to the Royal Palace and Theatre of Drottningholm where H. R. H. the Crown Prince of Sweden received the Congress Members on behalf of H. M. the King. | 7 p.m. | Dinner at the Castle of Uppsala. |
| July 13. | 8.15 a.m. Excursions to the Stockholm Archipelago. | July 17. | 9 a.m. Sectional Meetings.
2 p.m. Sectional Meetings. |
| July 14. | 9 a.m. Sectional Meetings.
1 p.m. Sectional Meetings.
8 p.m. General lectures. | July 18. | 9 a.m. Sectional Meetings.
1 p.m. Luncheon for the Honorary Presidents given by the City of Stockholm. |
| July 15. | 9.15 a.m. Second Plenary Session. | July 19. | 1 p.m. Sectional Meetings.
9 a.m. Sectional Meetings.
1 p.m. Sectional Meetings.
8 p.m. General lectures. |
| | | July 20. | 9 a.m. Sectional Meetings.
3 p.m. Third Plenary Session.
7 p.m. Farewell Party in the Town Hall of Stockholm. |

MEETINGS OF INTERNATIONAL COMMITTEES

The following meetings of International Committees during the Congress were reported to the Secretary General:

Botanical Section of the International Union of Biological Sciences, July 7th-11th.

International Committee on Palaeobotanical Nomenclature, July 7th-11th.

International Association of Wood Anatomists, July 18th.

PLENARY SESSIONS

MINUTES

Minutes from the First Plenary Session of the Seventh International Botanical Congress, held in the Concert Hall in Stockholm on July 12, 1950 at 10 a. m. in the presence of the Patron of the Congress, H. R. H. the Crown Prince of Sweden and representatives from foreign Embassies and Legations and from official Swedish institutions.

Present: Botanists from 54 countries.

The President, Professor C. SKOTTSBERG, in the chair.

Secretary: Dr. EWERT ÅBERG.

§ 1.

The President opened the meeting on behalf of the Organizing Committee and wished everyone welcome. In his address he gave an account of the work of preparation and organization and thanked authorities, institutions, commercial enterprises and private individuals for financial assistance. He then dwelt upon the world situation during the last fifteen years, its influence on the possibility of arranging an international congress and on the scientific work in botany and genetics in general, especially in countries directly engaged in World War II. Turning to H. R. H. the Crown Prince, he asked him to declare the congress open (p. 27).

§ 2.

H. R. H. the Crown Prince then took the chair. He bade all welcome to Sweden, contrasted modern specialization with the all-embracing outlook of a man like LINNÉ, expressed his best wishes for a successful meeting and declared the Congress open (p. 32).

§ 3.

The Secretary General of the Sixth International Botanical Congress in Amsterdam 1935, Professor M. J. SIRKS, thanked H. R. H. for his

very kind words of welcome. In his speech Professor Sirks revived the memory of those who took part in the Sixth International Botanical Congress but who were no longer amidst us and, in his closing words, paid tribute to the genius of Hammarby and to Swedish botany from the eighteenth century to modern times (p. 33).

§ 4.

The President read the following telegram to His Majesty the King.

"H. M. Konungen,
Solliden, Borgholm.

Sjunde Internationella Botanistkongressen, samlad i Stockholm och representerande 54 länder, bringar Eders Majestät sin varma, vördnadsfulla hyllning och uttrycker sin djupa tacksamhet för det storartade mottagande Eders Majestät behagat bereda densamma.

Underdånigst

SKOTTSBERG ÅBERG."

§ 5.

The Secretary General gave some information concerning the program of the Congress.

§ 6.

The President asked for proposals regarding the place for the Eighth Congress.

Professor P. CHOUARD issued an invitation for the Eighth Congress to be held in France.

Professor A. F. BLAKESLEE issued an invitation for the Eighth Congress to be held in the United States of America.

Dr. J. ROUSSEAU issued an invitation for the Eighth Congress to be held in Canada.

§ 7.

The President announced that the proposals would be referred to a Committee of Recommendations and Resolutions and again be brought before the Congress at its final plenary session.

On the Committee of Recommendations and Resolutions the following members were appointed: R. S. ADAMSON, F. BHARUCHA, A. F. BLAKESLEE, B. BOIVIN, V. J. CHAPMAN, P. CHOUARD, H. R. DESCOLE, A. S. FOSTER, F. E. FRITSCH, MARGARET FULFORD, I. Y. GLUSCHENKO, R. HARDER, R. HEIM, R. E. HOLTUM, H. HUMBERT, A. W. JESSEP, H. J. LAM, E. D. MERRILL, G. NEGRI, N. POLUNIN, J. RAMSBOTTOM, F. RAWITSCHER, F. RESENDE, W. RO-

BYNS, D. P. ROGERS, J. ROUSSEAU, W. RYTZ, M. J. SIRKS, A. C. SMITH, T. A. SPRAGUE, V. N. SUCATJEV, F. VERDOORN.

Professors C. SKOTTSBERG and HUGO OSVALD were to serve as chairmen of the Committee.

§ 8.

As there were no more proposals the President introduced Professor Dr. F. T. WAHLEN who delivered his address on "Botany and World Husbandry" (p. 34).

§ 9.

The President thanked Professor WAHLEN for his address and closed the session.

Stockholm, July 12, 1950.

EWERT ÅBERG
Secretary General

Seen and approved:

C. SKOTTSBERG, President of the Congress and Chairman of the Organizing Committee.

ROB. E. FRIES, Honorary Chairman of the Organizing Committee.

HUGO OSVALD, Vice President of the Congress and Vice Chairman of the Organizing Committee.

Minutes from the Second Plenary Session with the Seventh International Botanical Congress held in the Concert Hall in Stockholm, July 15, 1950 at 9 a. m.

Present: Botanists from 54 countries.

The President, Professor C. SKOTTSBERG, in the chair.

Secretary: Dr. EWERT ÅBERG.

§ 10.

The President opened the meeting and informed about the program for the day. He then introduced Dr. FRANS VERDOORN who spoke on the subject: "The International Plant Science Congresses" (p. 42).

§ 11.

The President thanked Dr. VERDOORN for his interesting and detailed account of earlier congresses and then introduced the next speaker, Dr. F. W. WENT, who spoke on the subject "The Effects of Climate on Plant Growth and

Distribution" (p. 56) and showed a colour film from the Earhart Plant Research Laboratory at Pasadena, California.

§ 12.

The President turned to Dr. WENT, expressed the audience's thanks for his most interesting account and declared the session closed.

Stockholm, July 15, 1950.

EWERT ÅBERG
Secretary General

Seen and approved:

C. SKOTTSBERG, President of the Congress and Chairman of the Organizing Committee.

ROB. E. FRIES, Honorary Chairman of the Organizing Committee.

HUGO OSVALD, Vice President of the Congress and Vice Chairman of the Organizing Committee.

Minutes from the Third Plenary Session of the Seventh International Botanical Congress, held in the Concert Hall in Stockholm, July 20, 1950, at 3 p. m.

Present: Botanists from 54 countries.

The President, Professor C. SKOTTSBERG, in the chair.

Secretary: Dr. EWERT ÅBERG.

§ 13.

The President declared the session open and read some messages received during the Congress. Among them was the following telegram from H. M. the King:

"Jag sänder Eder mitt hjärtliga tack för vänliga telegrammet och mina bästa välgångsönskningar till kongressen.

GUSTAF."

§ 14.

The President read the following telegram to H. R. H. the Crown Prince:

"H. K. H. Kronprinsen,
Sofiero
Hälsingborg.

Botanistkongressen, samlad till sitt sista möte, sänder sin höge beskyddare sitt vörd samma och hjärtliga tack för oskattbar medverkan till dess framgång.

SKOTTSBERG ÅBERG."

Further, the President read the following telegram to Professor L. H. Bailey:

"Professor BAILEY, Bailey Hortorium,
Sage Place,
Ithaca, N. Y., U. S. A.

The Seventh International Botanical Congress begs to thank the venerable President of the Fourth Congress and Senior Botanist of the world for his kind greetings and wishes him many more years of scientific activity.

SKOTTSBERG ÅBERG."

§ 15.

The President gave the word to Dr. E. D. MERRILL who in the name of the members of the Congress with a few words of thanks paid tribute to the memory of LINNAEUS and as an appreciation of the organization of the Congress in Stockholm presented a wreath of *Aucuba* leaves and white water-lilies to be laid on the tomb of CARL LINNAEUS in the Cathedral at Uppsala.

§ 16.

The President proceeded to a number of business matters, communications and resolu-

tions, which had been passed by the Recommendations and Resolutions Committee.

Mom. 1. The proposals for the Jakob Eriksson Prize Fund (Resolution 1, p. 63) were accepted. The following persons were appointed members of a special committee for the Prize Fund: Professor E. MELIN (chairman), Professors R. CIPERRI, E. GÄUMANN, R. HEIM, J. RAMSBOTTOM, E. C. STAKMAN and JOHANNA WESTERDIJK.

Mom. 2. A recommendation that a Commission for Plant Raw Materials be appointed and a resolution by the AGR section that a section for Plant Raw Materials be established at the next International Botanical Congress. Resolved in agreement with the recommendations (Resolution 2, p. 63).

Mom. 3. The decisions of the NOM section were accepted and the appointment of Standing Committees (Resolution 3, p. 64) by the section of Nomenclature confirmed.

This done, the President said: "I move that we tender our very best thanks to those who, in the first place, have devoted so much of their time to get together the Proposals for the Additions and Alterations of the Rules: Professor LANJOUW, Dr. JONKER, Dr. HYLANDER, and Dr. and Mrs. SPRAGUE." This was unanimously carried.

Mom. 4. Recommendations and resolutions from the PHG section (Resolutions 4-7, pp. 66-67). Accepted.

Mom. 5. Recommendations and resolutions from the TCR section (Resolutions 8 and 9, p. 67). Accepted.

Mom. 6. A recommendation from both sections for Taxonomy (TCR, TPH) that an International Association for Plant Taxonomy with a Bureau for Plant Nomenclature and Taxonomy (Resolution 10, p. 67) be established. Accepted.

Mom. 7. A recommendation by the Committee of Resolutions that a Section for the History of Plant Science be organized as part of the coming international botanical congresses (Resolution 11, p. 68), was accepted.

Mom. 8. A recommendation by the Committee of Resolutions regarding the meeting places for future international congresses (Resolution 12, p. 68) was accepted.

Mom. 9. At the first plenary meeting on July 12 three invitations to the Eighth Congress were presented and referred to the Resolutions Committee, which recommended the acceptance of the invitation from the French botanists. (Resolution 13, p. 68.)

Dr. JAMES M. SCHOPF, Columbus, Ohio, U.S.A., remarked that the voting in the Resolution Committee had given 15 votes for France against 14 for outside Europe, and that, consequently, the margin was so narrow that the question must be brought up before the plenary meeting for careful consideration. The President proposed that the assembly should vote in turn for Europe and for outside Europe by rising, which was accepted. The motion that the Eighth Congress should meet in Europe was carried with an overwhelming majority. Only a single invitation, from France, being left, the President moved that the Eighth Congress be held in Paris in 1954, the date proposed by the French delegation. This motion was unanimously carried.

§ 17.

Delegates from the nations represented offered their thanks to the Organizing Committee and to the Swedish authorities and expressed their high appreciation of the efforts which, in their opinion, had made the Congress a success. The spokesmen were: Professor H. BIRAND (East Mediterranean countries), Mr. A. A. BITANCOURT (Latin America), Professor A. F. BLAKESLEE, (U.S.A. and Canada), Professor F. BUSTINZA (Spain and Portugal), Professor T. DIANNELIDIS (Greece), Professor H. FITTING (Germany and German-Swiss), Professor F. E. FRITSCH (Great Britain), Professor R. HEIM (France and French Swiss), Professor H. LINDBERG (Scandinavia and Finland), Professor G. NEGRI (Italy), Professor A. A. PULLE (Netherlands and Indonesia), Akademiker V. N. SUCATJEV (U.S.S.R.) (Pages 69-76).

The Soviet Delegation presented to the President of the Congress a set of volumes of the "Flora of the U.S.S.R." for which the President expressed his sincere thanks.

§ 18.

The President addressed the members of his staff and committees and all the congress members present, thanking them for kind assistance and successful cooperation in organizing the Congress (p. 76).

§ 19.

The President introduced Mr. HALVAR SEHLIN of the Swedish Tourist Association who then gave a talk on "Swedish Nature and Culture" illustrated with autochrome slides.

§ 20.

The President thanked Mr. SEHLIN and closed the meeting with the following words: Mesdames, Messieurs,

L'heure du départ est arrivée. Beaucoup de vous prendront part à quelqu'une des excursions à Norrland et à la Laponie, la région de nos grands forêts, vastes marais et hautes mon-

tagnes, lesquelles, situées tant au Nord, présentent des paysages vraiment alpines, des formations géologiques et géographiques imposantes, des névés et des glaciers, et une belle flore alpine, une région où la culture n'a pas encore réussi à effacer l'impression ranimante d'une nature virginale. J'espère qu'il fera beau temps et que vous saurez apprécier le charme de la solitude. D'autres, je crois la plupart retourneront prochainement à ses pays natales. A tous de tout mon cœur: bonne voyage!

La séance est terminée.

Au revoir à Paris! Auf Wiedersehen in Paris! Well met in Paris!

Stockholm, July 20, 1950.

EWERT ÅBERG
Secretary General

Seen and approved:

C. SKOTTSBERG, President of the Congress and Chairman of the Organizing Committee.

ROB. E. FRIES, Honorary Chairman of the Organizing Committee.

HUGO OSVALD, Vice President of the Congress and Vice Chairman of the Organizing Committee.

ADDRESSES AND PAPERS

The President, Professor C. SKOTTSBERG:

Your Royal Highness, Distinguished Guests of Honour, Ladies and Gentlemen:

As President of the Seventh International Botanical Congress I have the privilege, on behalf of the Organizing Committee, to wish you all welcome.

Your Royal Highness! We are very happy to see our Crown Prince in our midst, and we want to express our warmest thanks to Your Royal Highness for having graciously consented to act as the patron of our Congress. We know that this is not merely a favour so often

extended to scientific bodies by Swedish Royalty: we are familiar with Your Royal Highness's sincere personal interest in botany and wide knowledge of the plant world, revealed also in beautiful gardens, lovingly tended with Your Royal Highness's own hands.

To the representatives from foreign Embassies and Legations in Stockholm as well as to the members of our Honorary Congress Committee who honour us with their presence, I present our respectful compliments.

Never before did a country with a population as small as that of Sweden act as host to an international conference equal in size and scope

to this botanical congress. Our membership figures, well over 1500, and distributed among 54 countries, leave all former ones far behind. It is certainly true that Botany is safely anchored in the Swedish mind, that our institutions stood firm behind our invitation, but we were not blind to the fact that we would have to face serious difficulties. The high cost of living, the general unrest and the precarious financial conditions in many countries, travel restrictions and barriers of all sorts, have made the organization of this congress a very complicated affair, and time has, indeed, not worked for us. Without the financial support from the Swedish Government we could not have succeeded. We regret that it has not been possible for the Prime Minister or the Ministers of Education and of Finance, to whom we are particularly indebted for the attention they have paid to our demands, to be present and to receive the expressions of our deep-felt gratitude. The Ministry of Defence gave us a helping hand by putting a number of naval craft at our disposal, thus allowing us to arrange several interesting excursions. The Foreign Department has done everything in its power to assist visitors from countries with which normal relations have not yet been established, to get their visa and entrance permits.

A question of the very first order was to find adequate localities for our headquarters, sectional meetings and exhibitions without having to pay rent. Most of these needs have generously been provided for by the University of Stockholm and its Rector, Professor CRAMÉR, as well as by the Rector of the College of Pharmacy, Professor OHLSSON.

Industries, business concerns and individual citizens have been kind enough to make contributions to the congress funds, some with a view of helping us to show hospitality. The Stockholm Brewers Ltd. will provide a picnic luncheon on the 15th; Kooperativa Förbundet, Nordiska Kompaniet and Mr. and Mrs. CARL CURMAN are largely responsible for the interesting and entertaining program we are able to offer the ladies of the Congress. A number of

medical men, interested in botany, have been kind enough to defray the costs of a visit to Skansen on Friday, the day after to-morrow. No visitor ought to leave our country without having seen this open-air museum of old Swedish culture, a monument of which we believe we have reason to be proud. The Stockholm City Council has invited the Honorary Presidents and the Presidents of the Sections to luncheon on Tuesday, and we shall all spend the evening of our last congress day in the magnificent City Hall, where, if the weather is good, you will enjoy the twilight on Lake Mälaren in beautiful surroundings; we regret that we must ask your assistance to cover the cost of the refreshments arranged for by the Congress itself.

The climax, however, will be reached already this afternoon, when you will be the guests of His Majesty the King, represented by His Royal Highness the Crown Prince, in the grounds of the castle of Drottningholm, the Versailles of Sweden, our finest example of classical French garden architecture and frequently the residence of His Majesty.

To everybody who, in one way or other, has given us his or her support, our most sincere thanks are due.

Fifteen years have passed since botanists from all over the globe met to renew old ties of friendship, to make new acquaintances and to work together in a spirit of goodwill and mutual understanding—fifteen years of anxiety and fear, bloodshed and destruction. We, who are old, mourn the golden age when peace was regarded as a normal state of things, when no barriers isolated the nations from each other, when we could go anywhere and feel that we were welcome—provided that we were tolerably decent people—and when an international congress could close its final session under the safe conviction that the next one would meet there and then. We said so when we parted in Amsterdam in '35; even if thunderladen clouds had begun to darken the horizon, nobody, at least not among us innocent botanists, could foresee what was to come. We passed a resolution that the Seventh Congress would meet in Stockholm in

1940. The preparations, under the guidance of professor ROBERT FRIES, were well advanced when the war broke out. When at last the tyrants had been slain, we beheld a world in ruins, bleeding, starving, sick unto death, with millions and millions of people driven from their homes. This was only five years ago, and in the Far East hostilities had not yet ceased. It would appear premature, in an atmosphere poisoned by suspicion, envy, hatred and blind nationalism, to try and call even *scientific* cooperation to life. As time passed, however, voices were heard telling us that Sweden, one of the very few countries that had emerged unharmed, ought to renew her efforts to bring the botanists together. To many people it must have seemed almost preposterous that our little country, with a voice like a timid whisper, inaudible in the concert of the big trombones, could stitch together the ties cut by the sword. When at last the guns had been silenced, peace was still lingering in the distance, everybody was absorbed in his own troubles, wealthy nations had been reduced to beggary, scores of scientific institutions had suffered badly, and the loss of life in the younger generations had been heavy. The prospect was anything but encouraging, but it was our duty to answer the call and take the responsibility. Of course, a feeling of insecurity never left us. Dark forces are aiming at the very root of our civilization, which is freedom of thought and speech. Not many weeks ago we began to wonder if once more the Stockholm Congress would end before it started.

Our Congress is international. All countries were asked to join. We wanted a full-voiced orchestra. Still, if we compare our files with the Cambridge and Amsterdam records, the differences are obvious. Three nations which, after centuries of dependency, had gained their liberty after the first world war, Esthonia, Latvia and Lithuania, are no more, their men of science, if still among the living, are scattered all over the world. Several countries represented at the last congress and still existing, are absent to-day. The reasons vary, in some cases the financial situation is not too good, strict

economy a necessity, and the distance to Sweden large. Thanks to a contribution from UNESCO we have been able to assist a small number of colleagues from war-stricken countries, a fraction only of the many who deserved to be helped. We are sorry that our possibilities have been so very limited. Another matter of concern is that there were, in other countries, distinguished botanists who *wanted* to go and who *could* go but were prevented from coming by a political system which believes in self-sufficient isolation as the proper road to progress. For this reason several old friends and colleagues who were among the first to apply for membership, have been obliged to withdraw their application. We shall remember them with sympathy.

At the last congresses the Union of Soviet Republics was absent, which was the more to be regretted as the Union, in 1930, had been the host of the extremely well arranged and successful International Congress of Soil Science, a dominion where Russians have been pioneers. Many botanists from foreign countries participated on this occasion and had the privilege of meeting and travelling with distinguished Russian colleagues. It is gratifying that the Soviet Union has found it possible this time to send a delegation. Unfortunately, the official announcement with the names of the delegates and the titles of their papers reached us so late that the Congress Programme was in press, but a special supplement will be provided.

Two names of states in our catalogue are new: Indonesia and Israel; others have got a new bearing, because they have changed their political status by cutting the ties that formerly bound them to a mother country. We trust that their full independence will act as a stimulus also in the field of plant sciences.

When we started to plan this meeting we were unable to overlook the possible effects of the war on the participation of a number of countries. We did not fear that former enemies would blankly refuse to meet, but we had every reason to expect that the general lack of money would reduce the number of participants to a

very small figure. In some cases we were right; Japan, for instance, is enormously underrepresented when considering the large number of prominent Japanese botanists. With regard to Europe, however, our pessimistic views have been put to shame.

Encore une fois les ondes de la guerre ont roulé à travers des plaines fertiles de la France, dévastant les monuments d'une culture ancienne, souvent inappréciables, laissant à la queue chagrin et misère. Il est vrai que les grands instituts botaniques ont été sauvés, mais la main lourde de l'invasion a du paralyser l'activité scientifique, et la publication des résultats des recherches, source d'information indispensable, a rencontré des difficultés presque insurmontables. Fidèle à sa destination de centre civilisateur, fidèle à la devise de la ville de Paris, "fluctuat nec mergitur", la France s'est levée, la reconstruction a été rapide, et nous avons la grande satisfaction de pouvoir souhaiter la bienvenue à une forte délégation française. La Belgique, l'Espagne, l'Italie, tous ont souffert de pertes sérieuses, mais le botaniste-voyageur à retour de ces pays a constaté que notre science y est florissante et que ses culteurs sont bien préparés à prendre part à la coopération internationale.

La Hollande, pays de surface petite mais berceau d'hommes de science de renommée universelle, a enduré son temps d'épreuve avec une ténacité et un héroïsme que tout le monde admire. Avec ferme résolution elle s'est retrouvée dans une situation nouvelle et difficile exigeant des efforts gigantesques avec ressources réduites. Et, quelle que soit l'évolution politique dans les Indes, connues jusqu'à hier sous le nom des Indes Néerlandaises, il faut que l'œuvre magnifique qui y a créé un centre de botanique tropicale, où tout le monde a pu travailler sous les plus favorables conditions, pourra continuer en collaboration fraternelle avec les peuples de l'Indonésie. Nous regardons le nouveau projet, dont nous connaissons déjà les premiers fruits, la *Flora malesiana*, comme un résultat des efforts combinés et un témoin de bonne volonté.

Notre Congrès reste profondément obligé aux délégués de Hollande qui se sont consacrés à des études minutieuses des problèmes pas encore résolus par les Règles Internationales de Nomenclature. Sous les auspices de l'Union Internationale des Sciences Biologiques et avec le support d'UNESCO, ils ont arrangé à Utrecht, il y a deux ans, une conférence préparatoire. Les résultats, rassemblés par le Rapporteur général dans un volume présenté au Congrès, forme la base des discussions dans la Section de Nomenclature.

Was das deutsche Sprachgebiet für die Entwicklung aller Richtungen der Botanik immer bedeutet hat, ist uns allen wohl bekannt. Wir hatten Grund zu fürchten, dass unüberwindliche Schwierigkeiten die Teilnahme unsrer deutschen und österreichischen Kollegen in diesem Kongress beinahe verhindern würden. Bedeutende Teile des deutschen Gebietes sind verheert worden, eine Menge wissenschaftlicher Einrichtungen fielen dem Krieg zum Opfer. Jeder Botaniker, ganz abgesehen von Nationalität oder politischer Anschauung, wurde tief erschüttert, als ihm die Nachricht gebracht wurde, dass Dahlem vernichtet worden war, ein Mittelpunkt der Botanik von weltumfassender Bedeutung, wo viele von uns erfolgreich gearbeitet haben. Zeigte sich auch glücklicherweise später, dass die Zerstörung nicht ganz so vollständig gewesen ist als wir zuerst gefürchtet hatten, so sind doch Tausende von unersetzlichen Typexemplaren, wunderbare Sammlungen von lebenden Pflanzen, hochmoderne Laboratorien und eine der allerreichsten botanischen Bibliotheken verloren gegangen. Während des Krieges haben viele wichtige Zeitschriften aufgehört, und der ganze Vorrat unentbehrlicher Sammelwerke ist vom Feuer verzehrt worden. Wie ein Ersatz für diese katastrophalen Verluste zustande gebracht werden kann ist eine wichtige Frage, mit welcher sich dieser Kongress beschäftigen muss.

Für die deutsche Wissenschaft schien die Lage nach dem Krieg trostlos; alles fehlte, nur nicht der Mut. Verarmt arbeiteten die Botaniker weiter, eine neue Generation steht bereit das zu Trümmern geschlagene wieder aufzubauen,

muss man auch vom Grunde aus anfangen. Es ist ein erfreuliches Zeichen der Erholung, dass wir viel zahlreichere deutsche Kollegen hier begrüßen können als wir erwarteten.

Every child is aware of the destructive influence of the conflagration on the British Empire. Referring to botany, was there a botanist who did not recoil with horror at the thought that during the infamous "Blitz" seats of science like the Natural History Museum or the Kew Gardens might become annihilated? Fortunately, the scientific losses were small in comparison, but it seemed that, when the war was over, the wealth of Britain was gone. We who have visited England right after the war know that in spite of hardships and privations of which people here in Sweden have no experience whatever, the British spirit was unquenchable, and that scientific research was going on wherever the Union Jack was flying. However, when I discussed with English friends the possibility of having a botanical congress as early as in 1950—don't forget that it took eight years before we met after the first world war—I got the answer that, alas, few British botanists would be able to come. Botanists are, as a rule, not very rich, and public funds were running low. Be this as it may, the British delegation, including men and women from all the Dominions and some of the colonies beyond the seas, is the largest of all.

I shall not dwell upon the calamities our neighbours, Denmark, Norway and Finland, met with in the hands of ruthless enemies. It goes without saying that all their courage and power of resistance was needed, but also that although they pulled through under the greatest sacrifice, scientific life was, for the time being, half starving, and that the difficulties make themselves felt to this day. Nothing, however, could keep our good neighbours from joining us. We knew that we could count on them. Geographically we belong together, our plant world is practically the same and has the same history, and we have always been used to work in close touch with each other. Naturally, the Scandinavian element, strengthened by our

friends from Finland, is a very conspicuous feature in this richly faceted crowd.

Another thing we were quite sure of when we were busy with our preparations: the United States of America, the country of unlimited possibilities and a great and unselfish helper in times of distress, would not disappoint us. Plant science, in every aspect, has a stronghold in the United States, second to none anywhere; it serves no purpose to try to deny that the New World has taken the lead, in the field of botany as well as in many others. It is a generous and hospitable world. I think we can satisfy ourselves that many nations and races have a share in what is called American science. Let me make one more remark. In no other country so much is being done to atone for the thoughtless ravages during bygone generations, by trying to preserve what is left of vegetation in a natural state. This is of paramount interest to everybody, field workers and laboratory men alike.

La América Latina, en tiempos pasados, era un campo favorecido para los botánicos exploradores. Entre ellos figuraban, como viene de mostrarlo el profesor Fries en su libro sobre la historia de la botánica sueca, dedicado a este congreso, muchos de mis compatriotas. Pocos sudamericanos se dedicaban a la ciencia natural. Al principio de este siglo cuando llegué por la primera vez a Argentina y fui a buscar mis colegas argentinos me encontré con puros extranjeros y no hubo casi nadie que había nacido en el país. Grandes colecciones viajaron a los herbarios en Europa, donde se publicó también la mayor parte de la literatura botánica, tratando casi siempre de sistemática y fitogeografía. Laboratorios con facilidades para estudios citológicos o fisiológicos no existían. Cuarenta y siete años después de mi primera visita, treinta después de la segunda, cuando no se observó gran cambio, me tocó la buena suerte de volver. Y ahora el cambio era radical, el desarrollo había sido maravillosamente rápido, dando origen a institutos modernísimos donde trabajan los hijos e hijas del país con problemas de suma actualidad. Esto para servir como un ejemplo

entre otros, presentado porque lo he visto con mis propios ojos. No es preciso ser profeta para constatar que la América Latina ha entrado como colaborador independiente e importante en nuestros empeños, ni que va a jugar un papel cada vez más grande en los congresos internacionales de botánica. Me es grato saludar a los distinguidos delegados de las países de América Central y del Sur. Es la guerra y otra vez la guerra que ha reducido el número de sus representantes. ¿No creen Vds. que el mundo se volvería más habitable si se dejara a nosotros los naturalistas la gobernación?

I have dwelt at some length upon the consequences of the war on science in general and botany in particular, as reflected by the composition of our congress. Time has not permitted me to mention more than a few of the countries represented. I had to select those which naturally come in under the aspect I regard as rather self-evident on this occasion.

It is a source of the greatest satisfaction that, in spite of all obstacles, we are together once more in an atmosphere of friendship, to review what has been done in plant science during these strange and unhappy fifteen years.

Botanister från när och fjärran,
Välkomna till Sveriges huvudstad!

H.R.H. THE CROWN PRINCE OF SWEDEN:

My very first words in addressing this vast gathering of botanists from all over the world must be to wish you all a most sincere welcome to the land of LINNAEUS. His name is LINNÉ in Swedish. It seems most appropriate that a botanical congress should assemble in LINNÉ's native country and exactly at a time of the year, when his own little plant, the *Linnaea borealis*—much beloved by himself—is flowering in our woods.

Without LINNÉ's basic and exploratory work I dare say we should not be gathered together this day of July 1950. But I also wonder what LINNÉ would have thought, had he been able to look into the future and to perceive the vigor-

ous growth of the seed he so carefully sowed more than 200 years ago. At that time it was still quite possible for a man to be master of more than one branch of science. And we all know LINNÉ's capacity for commanding a wide range of the different sides of Natural History. Thus I suppose that his ingenious mind—though perhaps for a moment taken aback by the infinite diversity of modern botany—nevertheless would have been able to grasp the situation.

Speaking generally it seems to me natural and unavoidable that, as time goes on, science should become more and more specialized. Science must in itself be unlimited. And more especially natural science will no doubt always be subject to this trend. In perusing the programme of our congress one single glance will confirm this statement. Everyone of you is a specialist because to be an authority on a subject means in our day to specialize intensely.

And yet does it not sometimes strike us all that by becoming specialists, and specialists alone, we may have lost something important, something that is vital. I am referring to that synthetic outlook, that faculty of being able to master a wide scope of human knowledge, so characteristic of LINNÉ, but no doubt much more easily obtained in his day than in ours. Do we not all of us feel exhilarated, even thrilled, when meeting a fellow traveller with wide knowledge and a really world-wide outlook, men and women commanding their own speciality, and yet having been able at the same time to break their own shell, as it were, and to obtain that perspicacity, which tends to give a wider and a more balanced outlook on life. Such individuals indeed must be considered lucky. For a nation they represent a great asset. For humanity in general they are indispensable, inasmuch as they shoulder a considerable part of the responsibility for coordinating mental and physical aspirations of the whole of our human race.

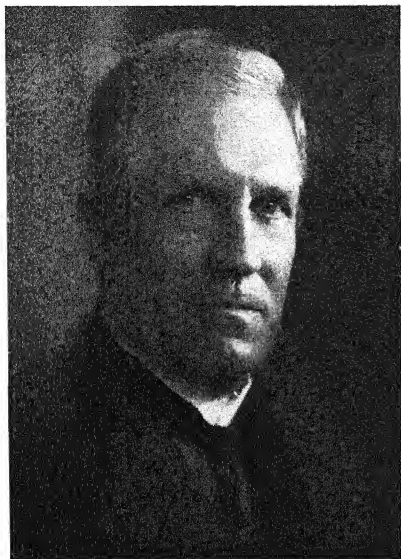
Returning, however, to the subject of this international congress one is indeed struck by the manifold aspects of modern botany. Though personally I am very little acquainted



H. R. H. the Crown Prince of Sweden declares the Congress open.

Photo: Dagens Bild.

PLATE II



ROB. E. FRIES.

Photo: Jaeger.



CARL SKOTTSBERG at the Opening Ceremony.

Photo: Dagens Bild.



ELIAS MELIN.

Photo: Sundgren.



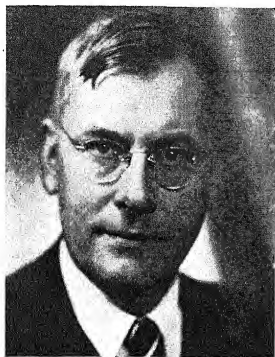
T. G. HALLE.

Photo: Wellinder.



HUGO OSVALD.

Photo: Ugglä.



CARL MALMSTRÖM.

Photo: Jaeger.



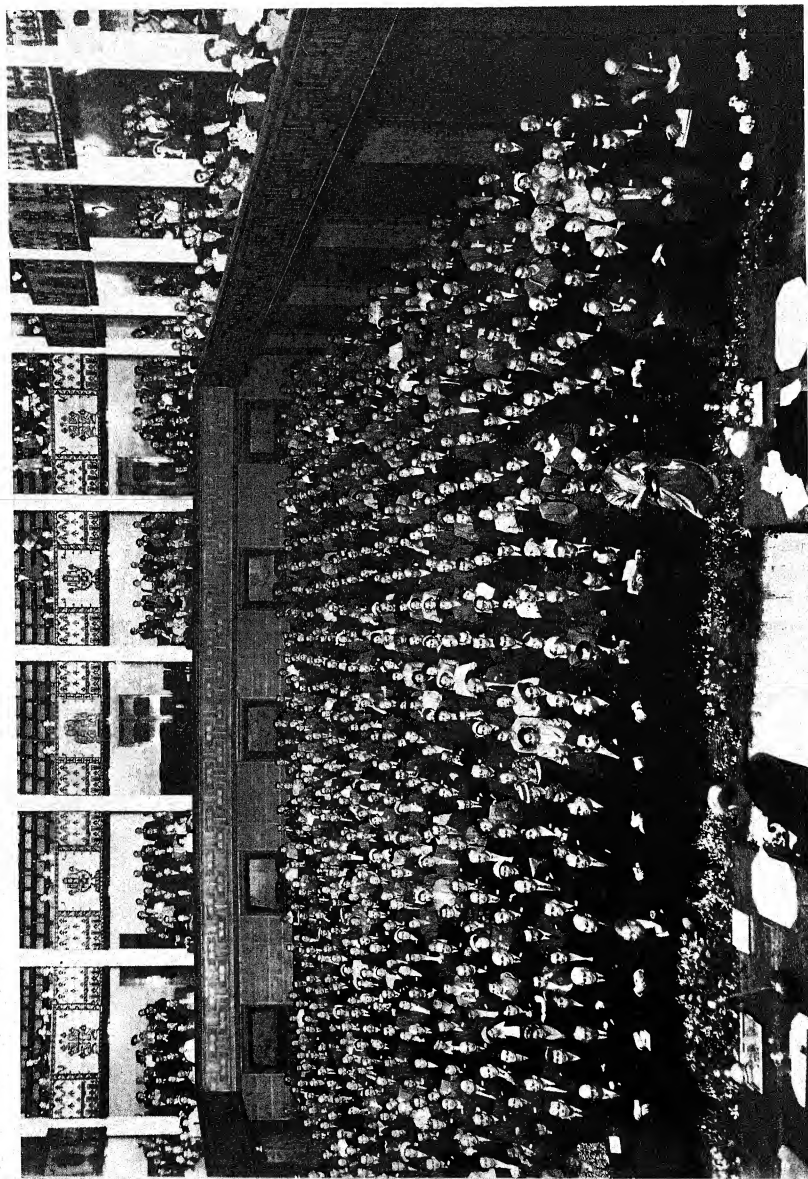
AXEL NYGREN and EWERT ÅBERG.

Photo: Aftonbladets Bildservice.



From a meeting with the Executive Committee and the Section Recorders. Sitting (from the left): LEVAN, TURESSON, Mrs. PRAVITZ, OSVALD, NYGREN, ÅBERG, SKOTTSBERG, ROB. E. FRIES, LUNDEGÅRDH, FLORIN, NANNFELDT, HULTÉN. Standing (from the left): LINDBERG, LINNELL, ÅKERBERG, ROMELL, NILS FRIES, BJÖRLING, MÜNTZING, BJÖRKMAN, FAGERLIND, DU RIETZ.

Photo: Sol-film.



The Opening Ceremony.

Photo: E. Boldt-Christians.

with most of them, I feel that they must all be of importance to science. And pure scientific research, even if it may look ever so theoretical or abstract, may well one day lead to results beneficial to the whole world.

Take one single instance, the case of genetics. From a very humble start it has not only grown into a vast subject of its own, but has also rendered extremely important services to the whole of the human race. You are no doubt all aware of the work being done also in Sweden in this field of research. Important practical results have thus already been obtained where agricultural plants are concerned. And more lately we have likewise turned our attention to the problem of improving the quality of our forests by selective or even purely genetic measures. Personally, I confess feeling extremely fascinated by this particular branch of your science because it seems to me to contain almost unlimited possibilities of the most far-reaching importance.

And now, linking up to my introductory remark, I again bid you all welcome to our country. We are very happy that so many of the world's most eminent botanists should at this time be gathered in Sweden. I express to you all my best wishes for the successful working of this big gathering and have the pleasure, ladies and gentlemen, to declare open the Seventh International Botanical Congress.

Professor Dr. M. J. SIRKS,

Genetisch Instituut Huis de Wolf, Haren (Gron.),
Netherlands:

Your Royal Highness, Gentlemen representing the Swedish Government and Swedish Scientific Institutions, Mr. President, Ladies and Gentlemen:

It is an extremely great honour to me to thank your Royal Highness with greatest respect for the very kind words of welcome you addressed to the numerous foreign guests attending this Seventh International Botanical Congress. I only regret that this honour falls to me, since our President of the Sixth Congress

held at Amsterdam in 1935, Professor SCHOUTE, passed away a few years ago.

Since that year 1935 the world underwent big changes; we all lived through a number of hard years, but we all are grateful now to have regained a more normal life and to have taken up again our scientific activities. In my quality of General Secretary of the Sixth Congress I was happy to welcome 1100 botanists from all over the world. Many of our old friends from that time are no longer amidst us. I may mention a few names of those, whose presence we enjoyed at Amsterdam, but whom we strongly regret not to meet again here: our colleagues ALLORGE, V. H. BLACKMAN, CHRISTENSEN, DANSER, DIELS, FEDDE, GRÉGOIRE, HARMS, Sir ARTHUR HILL, HOLMBOE, LINKOLA, MAIRE, REHDER, RENDLE, ROSENBERG, SAHNI, SAUVAGEAU, SCHOUTE, SEWARD, FRITZ VON WETTSTEIN, DE WILDEMAN and so many others.

However, numerous younger botanists have joined our ranks and we feel extremely pleased that among the 1500 members of this Congress so many nations are represented.

In your opening address, Mr. President, you mentioned the support given by the International Union of Biological Sciences with the help of UNESCO to its Botanical Section, its work on Botanical Nomenclature and this International Botanical Congress. I may assure you that the IUBS did this with greatest pleasure, and though I just retired as its President, I am convinced that the Bureau of IUBS in future will continue this policy as far as possible.

And, Sir, being one of the members of the delegations from the Netherlands, I may be allowed to put away for a moment my international task and to thank you most cordially for the very kind words of sympathy you addressed to my country in its present situation.

There are various reasons because of which we enjoy being here at Stockholm. Since the war Stockholm has become a centre of international gatherings; this Botanical Congress already is the fourth international congress in biological sciences held here. This is because we know the very cordial hospitality your City

is presenting to all of us. I was a little bit surprised to find among the papers distributed at the Congress bureau a guide "How to Feel at Home in Sweden"; I may assure you that we don't need such a guide at all.

The second reason is that we all know that the heavy burden of organizing such a large congress may rightly be entrusted to our Swedish colleagues.

But the main reason why we like to come here is that Sweden, and most especially Hammarby, may be considered the birthplace of scientific biology, because our Master, the Princeps Botanicorum CAROLUS LINNAEUS, lived and worked here. You may be convinced that we all are greatly indebted to his personality, his mind of a genius, his splendid activity. Those of us who have admired the rich collection of Linnaeana Your Royal Academy has under its trust, will easily acknowledge that we cannot enough appreciate the good care Your Swedish people gave to his remembrance. Personally, coming from Holland, I may be allowed to assure Your Royal Highness that we don't forget the years during which LINNAEUS lived in our country.

I may end by paying a tribute to the genius of Hammarby, to Swedish botany in the eighteenth and nineteenth century and in modern times.

Professor Dr. F. T. WAHLEN,
Food and Agriculture Organization of the United Nations, Washington, D. C., U.S.A.:

Plant Sciences and World Husbandry

Je sais apprécier à sa juste valeur l'honneur qui m'a été rendu en m'invitant à contribuer l'adresse d'ouverture de ce congrès. Evidemment, je dois la distinction de parler devant une assemblée si brillante à la position que j'occupe actuellement. Le Comité d'Organisation a sans doute pensé que c'est à l'Organisation des Nations Unies pour l'Alimentation et l'Agriculture qu'incombe en premier lieu le devoir de s'occuper des relations entre les sciences botaniques

et l'économie mondiale. La O. A. A. n'est pas une Académie universelle des sciences de l'agriculture, des forêts et des pêches. Nous avons, par la charte fameuse de Hot Springs, le devoir de veiller à ce que les ressources naturelles du monde soient conservées et utilisées d'une manière judicieuse, que la production soit améliorée et augmentée par rapport aux besoins de la population mondiale, et que la distribution des produits tienne compte du bien-être de l'humanité entière. En travaillant pour la réalisation de cette lourde tâche, nous avons besoin de la coopération très active des gouvernements. Mais c'est de la part de la science que nous attendons les instruments nécessaires. Notre organisation, loin de vouloir édifier un contrôle des organisations scientifiques internationales, attend la plus grande contribution de leur liberté d'action et de la coopération enthousiaste des chercheurs que seule cette atmosphère de liberté peut créer.

Le premier Congrès International de Botanique eût lieu peu d'années après l'apparition de l'Origine des Espèces, livre qui a exercé une influence plus grande sur les sciences biologiques que n'importe quel autre. A cette époque, c'était la biologie qui primait entre les sciences naturelles. Entre temps, la chimie et la physique ont fait des progrès extraordinaires. La synthèse a remplacé, en partie, les matières premières d'origine végétale; nous avons appris à maîtriser l'air et la physique nucléaire nous promet des sources d'énergie inimaginables. Comme résultat, l'homme est conduit à se sentir hors de la nature, maître de l'univers. En acceptant de parler ici sur le sujet qui m'a été suggéré, je me propose de faire ressortir notre dépendance de la nature animée, et nos responsabilités envers l'entité que nous constituons avec elle.

Die sich überstürzende Entwicklung der letzten Jahrzehnte hat manchen Einteilungsgrundsatz der Wissenschaften gründlich in Frage gestellt. Die Abgrenzung von Geisteswissenschaften einerseits, Naturwissenschaften andererseits, ist nicht mehr als deutliche Linie

erkennbar. Die Konturen sind auch fließend geworden zwischen den Gebieten, die man als reine und als angewandte Wissenschaften zu bezeichnen pflegte, vielleicht zum Schaden jener nicht zweckgebundenen Tätigkeit, die man besser als Fundamental-Forschung bezeichnen sollte. Chemie und Physik fließen zwanglos ineinander über, und die Virusforschung scheint im Begriffe zu stehen, eine Brücke zwischen dem belebten und unbelebten Molekül zu schlagen. So ist es denn auch kein besonderes Wagnis, vor diesem Kongress die *scientia amabilis* mit der trockenen Oekonomie zu vermählen.

Dieser 7. Internationale Botanische Kongress ist in der Tat nicht allein Angelegenheit einer engen Zunft von Wissenschaftlern, sondern er muss jeden Gebildeten interessieren und geht jeden Menschen direkt an. Man braucht sich nur zu vergegenwärtigen, welche Fortschritte in den letzten anderthalb Jahrzehnten seit dem 6. Kongress 1935 erzielt worden sind, und in welchem Masse viele davon einen direkten Einfluss auf das Ergehen der Menschheit ausübten. So ist es denn eine dankbare Aufgabe, vor einer so glänzenden Versammlung über den Platz und die Aufgaben der Pflanzenwissenschaften in der Weltwirtschaft zu sprechen.

Leider gibt es keine befriedigende Übersetzung für das schöne englische Wort "husbandry" in die deutsche Sprache. Der Begriff des Haushaltens, der darin neben dem des Wirtschaftens mitschwingt, ist für jeden besonders sympathisch, der die Aufgabe der heutigen Pflanzenwissenschaften auf ökonomischem Gebiet nicht in der vollen Bedarfsdeckung mit Nahrung und Bekleidung erschöpft sieht, sondern der sich darüber hinaus um die Erhaltung der Schönheitswerte der Pflanzendecke, die Erhaltung und Erhöhung der Fruchtbarkeit der Böden, und um die Zusammenhänge zwischen den erneuerbaren und nichterneuerbaren Rohstoffquellen bemüht.

Less than a year ago, the United Nations convened a Scientific Conference on the Conservation and Utilisation of Resources. This constituted the first joint effort to establish an

inventory of the world's riches, and an evaluation of our methods of using them. One group of conference delegates worked on the so-called non-renewable resources, such as minerals, coal and petroleum; the other on the renewable resources, including land, water, flora and fauna. Two results of this stock-taking are particularly noteworthy. The first is that our present knowledge of the world's resources is extremely inadequate. We are living on a bank account without a balance-sheet. This is the more serious since there exists no possibility to assess adequately the future rate of use. This rate depends not so much on the increase of the world population, which is rather uniformly expected to reach the figure of 3 billions by the year 2000 against the present 2.3 billions. A much greater immediate influence may be exercised by the standard of living as measured in units of consumption. If in the foreseeable future such rather rare metals as copper, tin and zinc were used in approximately the same quantities by all peoples as they are being used by the people of the United States, then the known reserves would be exhausted in a relatively short time. The same applies to petroleum. Such a development would make the relationship between renewable and non-renewable resources much more apparent than today, and would compel us to lay far greater stress on an expanded use and a careful husbandry of the renewable resources.

The second major result points in the same direction. Less concern was felt at the conclusion of the conference regarding the world supply situation of a number of non-renewable commodities, such as oil and coal, than had been voiced by some experts in the past. On the other hand, without taking the dismal outlook of some writers on the subject during the past years, genuine concern was expressed over the apparent inability of nations and the world as a whole to evolve permanent systems of sound husbandry for the conservation and judicious use of the renewable resources.

From an overall point of view, there can be no doubt that the plant scientist holds the key

to the greatest treasure-store humanity possesses. All life depends on the faculty of chlorophyll to combine three elements into organic matter with the help of solar energy, and on the faculty of plants to build up proteins. There is no process of energy transformation on earth that could be compared in magnitude with the process of assimilation going on in the myriads of green leaves. This process furnishes us with food, clothes, shelter and innumerable raw materials, and is the basis of all animal life. The organic remnants, in the form of humus, maintain and build up soil fertility. But plants are not only the chief providers of life's necessities. They bring beauty and joys untold into our existence, and they are the great regulators of the local climate and the water household. The plant cover of geological ages gone by has provided us with stored-up solar energy in the form of coal and petroleum, two of the key commodities of the industrial age.

Agriculture, and to a lesser extent forestry, is fundamentally concerned with the task of guiding these synthetic processes so that the greatest possible net effect in the desired form may be obtained. In spite of the progress achieved in the art and science of plant production, the process of transforming solar energy through chlorophyll remains at a very low level of efficiency. Under favourable cropping conditions, our chief economic plants store about 2-3 % of the radiated solar energy; under laboratory conditions, these figures may rise to 6-7 %, and in the case of some algae, the net energy effect seems to be very much higher. In the face of the possibilities suggested in these figures, we need not despair of the prospect that the earth may have to feed almost a third more people within the next fifty years. Indeed, if the land resources of the world were fully used today by applying present knowledge to the degree that obtains in the more advanced countries, we could easily raise nutritional standards all over the world to the desirable level, take care of the increase in population of about 700 millions expected in the next fifty years, and produce a vast amount of industrial raw ma-

terial and fuel which is now taken from resources that cannot be replenished. Although all such estimates contain a considerable element of uncertainty, it has been stated recently that apart from a better use of the land now under cultivation, something like 400 million hectares of tropical soils and 120 million hectares of land north of the temperate zone constitute potential reserves of crop lands. As further reserves we have the vast possibilities of improved ocean husbandry, and the enormous expanses of unmanaged forests.

There can be no doubt that the manner in which we make use of the material and the ideal riches invested in the plant cover of our planet will be one of the decisive factors in the welfare and happiness of mankind. It is of absorbing interest, therefore, to review past and future contributions of the plant sciences in this regard.

In attempting to do this, I should like to make clear at the outset that time limits prohibit any encyclopedic mode of treatment, and that the few examples used do not represent an attempt to evaluate the economic importance of the different branches of the plant sciences. I must admit that the title of this opening address, which was proposed by the Organization Committee of the Congress, contains a temptation to choose this mode of treatment, particularly as viewed from the angle of the Food and Agriculture Organization of the United Nations. Indeed, it would have been easy, and incidentally encouraging, to cite staggering figures in terms of present contributions of plant sciences to world economy, and to refer to their future possibilities. If this distinguished gathering were a sort of World Board of Trade, such an approach might be the proper one. We are here, however, to use these next days for a stock-taking, not in terms of kronor or dollars, but in terms of scientific veracity. The guide-posts to truth are question marks. The only apology I have to make is that some of the question marks that will be raised in this address may be further afield than may be customary on occasions of this kind. They concern the in-

dividual not only as a specialist in his field, but as a citizen of the world.

The first subject upon which I should like to dwell is the broad theme of land use, in which the plant ecologist, the agronomist, the horticulturist and the forester are interested along with the soil scientist, the country planner and the conservationist. Historically, the settling and use of land have been done largely on the trial and error method. Rising population pressure has often forced the use of land on the most intensive pattern, viz. by cropping, which was not suited either because of unfavourable soil characteristics, dearth or excess of water, or by limits imposed by other climatic factors. Much hardship for the people concerned and a great deal of destruction have resulted from such practices. In the old settled countries of the humid and semi-humid regions, the lessons of history have been learned and much damage has been repaired. Unfortunately, these lessons had but a very slight effect when most of the remaining land resources were settled during the last 150 years. Settlers relied entirely on the experience gained in their former, often wholly different, habitat. Land being plentiful and cheap, exploitation rather than husbandry was the guiding principle. I need not relate the results of this approach, which culminated in a destruction of natural resources on a scale hitherto unknown in the history of the world. Fortunately, there is a growing consciousness of these dangers. But this is not enough. Communities which have seen the very basis of their existence, the soil, carried away by wind and water erosion, are in no position to cope with the danger and remedy initial mistakes. Outside help is needed, but it is so costly that only economically strong countries can bring an adequate measure of it. It is surely gratifying to know that the dust bowl in the central United States has been restored by such help and aided by a series of years with favourable precipitation to a degree of fertility higher than before the dreadful years of the middle thirties. But it will be a much bigger, in many cases an almost insoluble task to do the same in economically

weak countries with a predominantly agrarian pattern of economy.

It is safe to predict that the last frontiers will be settled within the next 50 years. Must such mistakes be repeated? The answer is no, if full use is made of the advice which ecologists, plant sociologists and soil scientists can give. Potentially, the danger is great. I shall cite but a few examples.

Fair promise exists that the tsetse fly will cease to be an obstacle to cattle raising in Africa. Thus immense expanses of land not economically used so far will be opened for production. However, it must be realised that the tsetse acted as a powerful agent of conservation. Much of the land in question would be particularly vulnerable in the case of over-stocking or of other misuse. A thorough land utilisation study, including the study of plant associations and successions which largely determine the carrying capacity, is essential if mistakes are to be avoided. Such mistakes might be of immense consequence, because it is quite possible that under the natural conditions existing, and having regard to the scanty economic resources of the region, irreversible changes in the plant cover might take place which would be tantamount to destruction. In other areas, the elimination of malaria might open new lands. In all such cases, full use should be made of fundamental knowledge available, and in this connection I should like to stress the great importance of the closest cooperation between plant sociology and soil science, not only in a common approach to practical problems of this kind, but also in their basic research.

A particularly pertinent example in this connection is the use of tropical soils. Reference was made earlier to estimates that an addition of about 400 million hectares of tropical land to our food resources could reasonably be expected. Such estimates, although comprising only about 20 % of the total reserves, did not remain unchallenged. It is pointed out, for instance, that the fabulous fertility of soils under the luxuriant tropical high rain forests is in reality non-existent. The luxuriant growth

of these forests is based on a rapid turnover of plant nutrients in a cycle of decay and growth. Interrupt this cycle by the destruction of the plant cover, and all that remains is a thoroughly leached, senile soil without possibilities for the raising of annual crops. Thus we may have to limit the use of tropical lands for intensive cropping to soils of recent volcanic origin, and to alluvia, while it may become an important task to find and improve new tree crops as sources of food and feed, and for soil protection for highly degraded soils.

These few examples are sufficient to highlight the important contribution plant sciences are called upon to perform in the broad question of land use—whether for cropping, horticulture, intensive animal husbandry, forestry, grazing or for combined systems of husbandry. For the next step, we turn to another sector of plant science distinguished by great achievements in the past, and full of promise for the future. I refer to the choice of crop plants, their varieties, strains and provenances, and their improvement through breeding. Systematic plant exploration still holds out great promise. Of the 200,000 to 300,000 known species, less than 250 are cultivated as sources of food and fibre, or for other economic purposes. It is doubtful whether more than 20,000 are economically useful to any extent in such pursuits as forestry, grazing, gathering of wild plants or as sources of drugs.

Plant exploration includes not only the study of gene-centres, but the location of species for new purposes. Strangely enough, the most spectacular plant exploration of recent years did not take place in a remote corner of the world, but in the laboratory. Penicillin, streptomycin and aureomycin are witness to the fact that species which were just moulds yesterday were turned into highly important laboratory crops. So plant exploration in the widest sense, backed by anatomical, physiological, chemical and genetic studies of the vast reservoir of plants of which we know not much more than the names, still holds out great promise. Nutrition surveys in the homes of aborigines in Africa

and elsewhere revealed that the intake of calories and protective food, including vitamins and mineral salts, seemed to be on an astoundingly low level until it was discovered that these tribes complement their diets by what may be termed "browsing" in the forest, bush and savannah. Some tribes use fruits, roots or leaves of three to five dozen wild growing species during the course of the year. An inventory and analysis of such plants might be a very worth while undertaking.

As an agronomist, let me turn in this connection to a more closely defined group of plants with great potentialities, the grass family. Needless to stress here the great role this family plays in world economy. The major bread and food crops, ranging from wheat and rice to sugar-cane, belong to it. The *Gramineae* also include some of the most important forage and pasture plants, used either in cultivation or as semi-cultivated and wild species. It is noteworthy that in many countries the decisive role of these grasses in the establishment and maintenance of a permanent agriculture was recognized but recently. Grassland agriculture is a comparatively new term. Its goal is the judicious use of grasses as sod crops in a proportion suited to the natural conditions and the economic needs of a region and in a manner that will safeguard the permanent fertility of the soil. There is no safer road to an agriculture that can satisfy indefinitely mankind's needs of food, fibre and raw materials than grassland farming, because there is no agricultural crop that fulfils the demands of soil protection and soil conservation better than do the grasses. Using the term grassland agriculture in its wider and generally accepted sense, there is no crop that has wider usefulness in restoring fertility and desirable soil structure, and in maintaining organic matter in soils under rotations, than grasses and legumes grown in association. Undoubtedly still fuller use can be made of the qualities of grasses by breeding, by introducing new species for special purposes such as the restoration of depleted lands, the fixing of sand dunes and the filling up of inland

and tidal marshes. The help of the plant sociologist is required to investigate the potentialities of the natural grasslands, which cover more than a third of the world's land surface. He can make a further great contribution in the study of the dynamics of such artificially established associations as temporary and permanent leys, and of their beneficial effects in rotations. It is worth while remembering that some of the earliest and fundamental work in plant sociology was done on meadows and pastures. There is also need for an overall sociological approach to the many intricate rotation problems. Raising a question in a very unorthodox manner, should we not more than in the past consider the sequence of crops included in a rotation as an artificial association separated into its components and spread over a number of years? We need a wider understanding of the interactions of crops following each other in relation to the household of water and nutrients, to the effect on soil structure and soil biology, including the questions of pathogens, and in relation to the reactions of crops to plant excretions.

Among the different branches of plant sciences, the improvement of crops by breeding is perhaps the one in which the evaluation of economic results was most often attempted. A large array of figures exists in individual countries on per cent increases or increases in yield over a period of years, or in terms of dividends earned by the national economy on the modest investments made for the creation and upkeep of plant breeding stations. All these attempts meet with an analytical difficulty. Progress has been simultaneous on many fronts, and to a large extent interdependent. Better fertilization of soils, improved methods of cultivation, control of insects and diseases have superseded less efficient methods concurrently with the advent of varieties with a higher yielding capacity, and it is difficult indeed to assess exactly the contribution of each of these factors. However, there is no more powerful motor to bring about efforts to improve all growth-factors subject to influence than the availability of varieties which are potentially able to turn these improvements

into yields higher to an extent sufficient to pay for the additional costs and to leave a profit. In this connection the question has often been discussed whether future plant breeding will bring results comparable to those achieved in the last decades, or whether at least for the crops on which much work has already been done there will be a certain slowdown. It has been said that the first great strides in plant breeding were the easiest, because simple methods such as line-segregation in self-fertilized crops were apt to yield spectacular results in a relatively short time. Greater knowledge, greater effort and better equipment are required to-day to realise the same amount of measurable progress. But it would certainly be unrealistic to assume that future progress will be slowed down. For one thing, many crop plants have hardly been tackled by the plant breeder. In the further improvements of others, which have received a great deal of attention in the past, new methods have been evolved and the army of qualified plant breeders is growing more numerous every year. While the actual contribution of the individual may be smaller, because many of the modern methods are much more time-consuming, the combined progress of each decade may be even more marked than in the past. There is, however, one significant difference between the past of plant breeding and its future, apart from the scientific and technical side, which must be mentioned. The early days of plant improvement were the days of the lone achiever. One gifted individual, endowed with a sharp eye and an acute sense for essentials in plant life, was able to work wonders. The future belongs to cooperative effort. More and more shall we see teams of cytologists, geneticists, plant pathologists, physiologists and plant breeders working in closest cooperation. This in turn calls for a certain coordination of effort, both on the national and international levels. I am fully aware that the coordination of research raises many difficult questions. Some fear that it endangers the necessary freedom, and point to a certain incompatibility of the temperament of many born

researchers with any sort of regulation. Time does not permit discussing this point, but I am fully convinced that these difficulties must and can be overcome if they are approached in the right spirit by all concerned. After all, we must realise that science is so essentially a social pursuit that the individual accomplishes little without the help of others.

Sound cooperation not only ensures the maximum of results with a minimum of cost and effort; it is conducive to an overall stock-taking of problems facing the plant breeder today in common with many other workers in applied biology. I shall mention only briefly three of these problems in relation to plant breeding. Many of us look with growing concern at the chemical warfare which farmers and horticulturists are forced to wage today against insects and diseases if they want to secure their share in the markets and make a success of their chosen profession. The whole problem is extremely complex and no one single road will lead us to a more natural and harmonious control of pests and diseases. But breeding for resistance is surely one of the most promising lines of attack. We must vigorously pursue it not only as a means of increasing production and lowering costs, but as a step in restoring the maximum approach to equilibrium in nature compatible with human needs.

Another problem in need of more attention is the nutritional quality of foods from the highest yielding strains of crop plants. Attention is focused on this problem as soon as the missing quality interferes with the processing of products. For instance, insufficient baking strength of some mass-yielding wheat varieties is well known, and is being successfully corrected. But we know too little of the finer biochemical structure of foods produced from mass-yielding strains, and should call on the nutritionist and bio-chemist to bring more light into the complicated inter-relationships between quantity and quality.

This leads to the third point, which is a consideration of the question as to which degree of agricultural intensity may be compatible with

the overall goal of a permanent and stable husbandry, serving not only the producer but humanity as a whole. Varieties and strains with a high-yielding capacity demand a favourable environment, which means the best of care and high fertilisation. If these conditions are not assured, they may bring smaller yields than the more primitive varieties from which they sprang. Thus they tend vastly to accelerate the rate of intensification. The process is too recent to allow us sufficient observations to form an opinion regarding the ultimate effect of these practices on the permanent fertility of soils. In this connection also we must try to observe and think not in terms of our lifetime, but in terms of world husbandry for future generations.

The contribution of plant physiology to the economic progress of the world has repeatedly been noted in passing. Plant nutrition has perhaps produced the most notable advances during the last two decades in pointing to the application of trace elements as a major corrective for soils of naturally low fertility, and in the use of radio-active isotopes in fundamental nutrition studies. The use of trace elements, mostly along with phosphates, is in some cases the key to the opening of new lands of very low fertility for production. Southern Australia is a good example. Intensive research has revealed in turn deficiencies in manganese, copper, zinc and molybdenum in different regions. The marked effect of burning in the tropics points to the probability of similar deficiencies in these highly leached soils. Observations so far gathered with the application of these elements point to numerous interactions in nutrition effects. Fortunately the technique of experimental design has kept step and permits the multi-factor approach to plant nutrition and other problems of crop production. New methods of detecting deficiencies in the plant itself, such as the spectrographic analyses of leaves, furnish the necessary instrumentarium for the handling of the large numbers of field samples incidental to the multi-factorial design of experiments. It is hardly overstating the case if we speak in this connection of the be-

ginning of a new epoch. The more the complexity and interdependency of growth-factors are realised, the better shall we understand why plants were not able to give a conclusive answer to many of the single-factor questions asked by the experimenter in the past. The multifactor experiment is one way of recognizing, in the biological sciences, the old truth that the whole is greater than its parts. It is one way to heed the sage admonition that we must work with, and not against, nature.

In my opening remarks, I referred to the United Nations Scientific Conference on the Conservation and Utilization of Resources. As time goes on, and as the exhaustion of non-renewable resources begins to be a reality instead of a spectre, the situation will no doubt be met by the inexhaustible resourcefulness of the human mind. In this battle for survival, plant sciences will certainly play a major rôle. In fact, they would be ready to play this rôle today if the economic laws governing the use of our heritage in natural resources could be made to fit more closely with the principle of conservation rather than exploitation and waste. A movement with an excellent aim and a badly chosen name, called "chemurgy" in the United States where it originated, is investigating the possibilities of using agricultural products and wastes as raw materials for industry. An imposing list exists of processes already proven on at least the scale of pilot plants or in large-scale production during times of emergency. Some are much older, of course, than chemurgy itself, such as the manufacture of industrial alcohol from starchy plants. But in this connection the question is raised: Should we not use alcohol as a fuel instead of using up the last reserves of petroleum? This query involves not only the conservation of oil-reserves, but is intimately linked up with one of the most bothersome problems of world economy, viz. the reasonable use of local agricultural surpluses, and thereby to the removal of a very important cause of cyclic economic depressions. Alcohol incidentally can replace petroleum in the manufacture of butadiene, the stepping stone to

synthetic rubber. Thus the production of starch, foremost of plant products, may replace the much sought rubber plant of the temperate zone. In the same trend of thought, the world's forest reserves assume a huge importance, as do also cellulose farm waste materials. Countless synthetic products emerge from the transformation of carbohydrates and plant proteins. The soybean, one of the interesting plants in this connection, has conquered America in a short time, but it has not nearly reached the limits of its usefulness.

No one can predict the time when changed economic conditions will bring forward urgent calls on the plant sciences to bridge gaps with these and other methods as yet unknown. The micro-biologist may step into the position of major producer of proteins and fats, and the algologist may have to evolve a technology for marine farmers.

In concluding, let me briefly make two remarks. It may have appeared from the presentation that undue emphasis was given to applied, at the expense of basic, research. This impression should not go uncorrected. It stems from the subject treated rather than from attitude. The importance of fundamental research as the fountainhead of technological progress cannot be overstressed. There is a danger today that governing bodies of institutes overstress the importance of research tied to an immediate economic goal, without realizing sufficiently that today's practical realisations would not be possible without the background of preceding fundamental research. The researcher's aim is truth, and society will be well advised to allow a sufficient number of workers to search for truth without relation to an immediate economic aim, but for the sake of truth itself. In due time, technology will turn their findings, no matter how theoretical they may appear, into applications undreamed of.

The second and concluding remark concerns the position of the scientist in modern society. Whether he wants it or not, his is more and more the rôle of the leader highly responsible for the fate of humanity. In this rôle he dare

not overlook one of the alarming features of our time, which is the growing disparity between ethical behaviour and material possibilities of modern society. We have not yet learned to bring to fruition the high moral principles evolved thousands of years ago, but we are quick to apply, for better or worse, yesterday's scientific discoveries. This implies a responsibility much broader than we have been ready to acknowledge in the past. I know that, particularly since the advent of man-induced nuclear fission, many leaders in scientific thought have wrangled with this problem without finding an answer. Perhaps there is none conclusive enough to satisfy. And yet our duty clearly is never to tire in searching for an answer, taking heed of the angel's promise in Goethe's *Faust*:

*"Wer immer strebend sich bemüht,
Den können wir erlösen."*

Dr. FRANS VERDOORN,
Chronica Botanica Co., Waltham, Mass., U.S.A.:

The International Plant Science Congresses, their History and Aims

*Come, Isabel, come to the soirée
Where Flora is placed in the chair;
Should you miss it, I'm sure you'd be sorry,
For all the beau monde will be there.
Only think that for four days together
Rare people, plants equally rare,
'Midst an odour of greenhouse and heather,
Will gather à plaisir et se plaisir.
We shall hear of great progress in walking
'Amongst plants once restricted to crawl ...
Of lache, inuendo, and scandal,
Of the wreck of some très bel espoir;
How the Tallow-tree held out a candle
To the gentleman vêtu de noir ...
Come, Isabel, child, are you ready?
I'm getting impatient, I own ...*

(J. R. C. in *Pall Mall Gazette*, 1866)

With your permission, I will open this account of the development of the 26 previous international gatherings of those concerned with the study of plants and plant life with a few general remarks:

"In the first place, our thoughts turn with pity to those botanists and horticulturists who wanted to come and who were prevented from doing so, either by their public duties, or else by the unfortunate state of affairs now existing on the continent. But let us set aside these personal considerations and rather congratulate ourselves on the prosperous state of the science of plants and its applications ... a prosperity of which this international gathering furnishes proof. In this respect, our age is a great age. Our knowledge of plants has been refined to an extraordinary degree of perfection, and science has been greatly advanced.

"What science wants, above all, is liberty—above all, that liberty which can be accorded to each individual only by public opinion. Science prospers only when national institutions and public opinion allow it freedom.

"Will other International Congresses spring up in the future? We must hope for that as well as for something even more important—peace. Imagine the cost of the millions of soldiers massed together at the present time ... You will find, that with their pay for a single day ... we could construct a conservatory reaching from Paris to Berlin."

This entire prologue, Ladies and Gentlemen, is not mine but part of an address with which ALPHONSE DE CANDOLLE, almost a century ago, in 1866, opened the International Botanical Congress and Horticultural Exhibition, in the London Guild Hall. Times change, and we are supposed to change with them; but the basic problems of mankind seem to remain rather stable. ...

Though the first international botanical congress was not held until 1864, our congresses antedate those of the zoologists, who began their international congresses in 1889; or those of the chemists who had their first international gathering in 1892. Before 1864 there were, of course, regional meetings, such as those of the *Deutsche Naturforscher* and the Scandinavian Naturalists, which drew visitors from all of Western Europe. In *Flora* for 1820 (Vol. 3, p. 746-748), I found what must be one of the earliest pleas for an international gathering of botanists.

Other phases of international coöperation amongst those concerned with the *scientia amabilis* date back much farther. Before 1800,

SCHRADER gave his generation what to-day we would call an international botanical newsletter: his *Journal für die Botanik*, with *Intelligenzblatt*.

Extensive international exchanges of specimens were organized in the first part of the past century by such men as OPIZ, the Botanical Comptoirs of HOCHSTETTER, HOHENACKER and others, the Unio Itineraria, and the Foreign Exchange Club of the London Botanical Society. The Verein für Mikroskopie of Giessen organized a world-wide exchange of slides and pharmaceutical specimens prior to the 1860's. MARTIUS' splendid *Flora Brasiliensis* shows us that international coöperative floras and manuals are not innovations of the 20th century.

In 1846, OPIZ proposed a 'Pflanzenakademie mit Normalherbarium,' a project which does not differ much from the international bureau which HALL proposed at our Cambridge Congress in 1930, and which Dr. LANJOUW and his associates are considering at the present time.

Four years before the first international botanical-horticultural congress convened, RABENHORST proposed some kind of international scheme to support the needy relatives of deceased colleagues.

Around 1842, at one of the meetings of the Deutsche Naturforscher at Mainz, SCHULTZ of Bipont outlined, at length, the need for the international index which we later received in the form of the *Index Kewensis*. At the same meeting, MARTIUS proposed an international abstracting journal such as those which we later obtained in the *Botanisches Centralblatt* and *Botanical Abstracts*¹.

The international exchange of journals and library duplicates was intensified towards the middle of the past century, and the possibilities of a society for the international exchange of reprints, a proposal which, with many modifications, has been cropping up for more than a

century, was also first discussed at the Mainz meeting in 1842.

A long time before we had our first international botanical address books, GISTEL issued his international directories of naturalists.

When formulating "unsolved questions" or "queries" in the Botanical Section of HERSCHEL's *Manual of Scientific Enquiry*, HOOKER and HANBURY emphasized, in several instances, the need for closer international coöperation in solving certain problems.

Nomenclature which, RAFINESQUE once said, will "never be permanently fixed until all errors are explored and corrected," was surprisingly little discussed at the early semi-international botanical meetings. Can it be possible, I sometimes ask myself, that LINNAEUS gave us a more stable basis than did DE CANDOLLE?

*

Ornamental horticulture—as an art, as a trade, as a science, as well as the fashionable pursuit of gentlemen of leisure—had reached an all-time high in the 1860's in Western Europe, particularly in the Low Countries, in England, and the regions around Paris and Hamburg. The staging of local, national and semi-international horticultural exhibits had been refined and perhaps reached its zenith—if we are to judge from eyewitness accounts of some of the large exhibits of the past mid-century, they seem almost unbelievable. Most of those engaged in ornamental horticulture, whether as professionals, as amateurs, or as scientists, were relatively wealthy in Victorian times. There were many huge, private conservatories, the owners of which supported a vast amount of plant introduction work, particularly of orchids. There was also a genuine interest in the phenomena of plant life, and horticulture and botany were closer in those happy days than they are at present.

In ÉDOUARD MORREN, the distinguished director of the Botanical Institute of the University of Liège, we find these times almost perfectly personified. About 1860, MORREN had organized the *Fédération des Sociétés d'Horticulture*.

¹ I have published in *Farlowia* 2: 71–82 (1945) the very instructive history of the last years of the *Centralblatt* under LOTSY and the beginning of the *Abstracts* under SCHRAMM and how it happened that the two international projects were not combined.

ticulture de la Belgique which organized, in Brussels, under his direction, the first of a series of international exhibits. With minor variations in the name, the series of exhibits and congresses, founded by MORREN, was continued to be called the "International Horticultural Exhibits and Botanical Congresses." It was MORREN's idea to hold them once every year, in one of the Western European countries, on an alternating basis, and under the auspices of his "Fédération" which functioned as a hold-over and interim organization.

Active ÉDOUARD MORREN, the son of CHARLES MORREN, whose name is also well-known in the annals of botany and horticulture, was a gracious gentleman botanist, and had many interests. Some of us know him as a great authority on the Bromeliads, others as the editor of the *Revue Belge Horticole*, for which he wrote so many articles and unique biographies. Others remember him for his work on the stomata or as editor of the *Correspondance Botanique*, our first international botanical address book which went into ten editions. The post office knew him as recipient of the city's largest foreign mail and the local aristocracy as the hospitable owner of a charming villa with a beautiful conservatory.

As an editor, scientist, and very active member of many horticultural organizations and councils, MORREN exerted world-wide influence and had numerous friends and admirers amongst scientists as well as amongst wealthy amateurs of distinction and in the trade. With their aid he was able to make not only an éblatant exhibition of the first Brussels Congress of 1864 but also a significant gathering of great botanists and horticulturists of his time. We honour him as the founder of international plant science congresses.

The combination of international horticultural exhibits, mostly of a high scientific standing, with a gathering of distinguished scientists from all corners of the western world, gave our early congresses that characteristic atmosphere which we indeed miss in our botanical and horticultural congresses of to-day.

Recently, late one enchanting California evening, I was preparing an exhibit at the Pasadena flower show. While I was arranging a number of prints of early classic flower shows and gardens, and as the nurserymen and horticultural amateurs of Los Angeles County drove in with their cars filled with the results of their endeavours, it went through my mind that the lives of most of us are like flower shows: days and weeks, if not months and years of hard, preparatory work for a show of brief perfection. Many of us have taken part, at some time in our lives, in the organization of a horticultural show. There is always something fascinating in them. Whether they be large or small, they hold some spell which we miss in our daily routine in the greenhouse, laboratory or library.

In the early congresses, the president was usually either a nobleman, a secretary of agriculture or a distinguished foreign visitor. The vice-presidents were, as now, distinguished foreign visitors. At the first congress they included BRONGNIART, FÉE, KOCH, PLANCHON, REGEL and REICHENBACH. There were 12 sessions (séances), each of them devoted to a group of "questions" which ranged from acclimatization (in which SIEBOLD, who had also made a wonderful exhibit of his introductions from Japan, played an important part) to the "Histoire de l'Horticulture". During the first Congress, many papers were delivered on the potato disease which was a most serious menace at that time.

The most distinguished visitors received the "Ordre Léopold," but "Décorations pour les travailleurs agricoles" were also awarded.

The early congresses did not pass any formal resolutions, though proposals on matters of urgency (e.g., the standardization of the names of vegetables) were discussed during the meetings.

*

The next year, in 1865, the 2nd Congress and Horticultural World Exhibit were organized in Amsterdam. Professor OUDEMANS was president. There were now 2 sections: one for horti-

culture, and one for botany. The Botanical Section met under the presidency of Professor FÉE of Strasbourg who was elected during the Congress. No lengthy, preliminary airmail consultations seem to have been necessary about such appointments in these happy, early years. There was an extensive discussion on the "Aims of Botanical Gardens" which makes still timely and inspiring reading. FÉE, MORREN, LECOQ, MIQUEL, REGEL, HOFFMANN, and others took part. GOEPFERT later contributed to the Proceedings of the Congress a detailed report on the Breslau Botanical Garden which was, at that time, one of the most elaborate and diversified gardens in the world.

KOCH spoke on Botanical Nomenclature, KARSTEN on *Cinchona*, and there was much in the programme dealing with the origin and functions of stomata.

In the Horticultural Section, DE BEUCKER's root grafts aroused considerable interest.

The third of our congresses was held in 1866 in London under the presidency of ALPHONSE DE CANDOLLE, from whose opening words I have just read you a few sentences. Preparations for the Congress had been made by SEMMANN who, when he had to depart on one of his Central American trips, was succeeded by MAXWELL MASTERS.

In the reports of this Congress we find the first public discussion of a large, coöperative project along international lines: the continuation of WALPERS' *Annales Botanices Systematicae*, for which collaborators as well as funds were needed. Professor KOCH went to great efforts to gain support for WALPERS but was not successful. WALPERS later committed suicide and the surplus funds, which accrued from the Exhibit, were used to acquire LINDLEY's Library for the Royal Horticultural Society.

The fourth Congress, which was held in 1867 in Paris in the building of the French Horticultural Society, played a very important rôle in the history of botany. It was at this meeting that the DE CANDOLLE Rules of Botanical Nomenclature, after discussion and some modification, were adopted. Under the name of

Paris Code or *de Candolle Lois* they were to guide a generation of plant taxonomists.

The fifth Congress was held in 1869 in St. Petersburg, through the efforts of REGEL, editor of *Gartenflora*. Born in Switzerland, REGEL had gone at an early age to Russia where he had charge of the St. Petersburg Botanical Garden and stimulated the horticultural endeavours of the Russian nobility. Two reports were published (as of several of the early congresses): one consisting of 243 pages by the Russian organizing committee; and another, a 112-page report, by the Belgian Federation, the mother organization of our early congresses.

The war of 1870 caused the first interruption in our congresses. But there was a congress again in 1871, the sixth, in London; and in 1873 there were two somewhat competitive congresses: one in Ghent and one in Vienna (the latter in connection with the Wiener Weltausstellung). The Fédération Belge recognized both congresses and reported about both of them.

World exhibits usually stimulate special, so-called international horticultural shows. Directly or indirectly in connection with these, official or unofficial, international or semi-international congresses dealing with the pure and applied plant sciences are also stimulated. Some of these congresses have been very important and useful; others, which have been arranged in a hurry and were of a semi-international character, have been harmful to the regular, international botanical and horticultural congresses.

In 1874, the 8th International Congress was held in Florence on the occasion of the Mostra Internazionale di Orticultura. This Congress, under the presidency of Professor PARLATORE, was the first which called itself "Congresso Internazionale Botanico." Young HOOKER, ALPHONSE DE CANDOLLE and RADLKOFER, who had developed into the "Kongress-Löwen" of their time, again played leading parts. Special sessions were held in Montferrat, Vallombrosa and Pisa, whither the members went in a special train. This is the earliest reference that I have found of such a special train at one of our congresses. There were also many excursions to

the old and beautiful gardens of the Florence region.

Then followed other congresses in Cologne (9: 1875), Brussels (10: 1876), Amsterdam (11: 1877), which also welcomed "Négotiants et Producteurs."

The 12th Congress, held in Paris, at the time of the Exposition Universelle of 1878, was very elaborate and attracted, for the first time, a good number of members from outside Europe.

Then, there came a series of simpler congresses, sometimes not too well prepared: Leyden (13: 1879), Brussels (14: 1880), Antwerp (15: 1881), and Ghent (16: 1883). The Ghent Congress, held in conjunction with the famous *Floralies Gantoises*, was of a purely horticultural nature, and it is considered by the Commission for the International Horticultural Congresses as the first International Horticultural Congress (the second official horticultural congress was held in Paris in 1889 and the third in Paris in 1900, both independent of the international botanical congresses, organized in those years in Paris).

In 1884, the 17th Congress assembled in St. Petersburg. It was much better organized than the 1869 Congress had been. There were, as at most of the early congresses, 2 sections: pure botany and horticulture (this time called applied botany). Many European visitors enjoyed meeting such famous Russian colleagues as MAXIMOVICZ, who reported on his explorations of Mongolia and Thibet, and TIMIRIAZEV who summarized the state of contemporary knowledge of chlorophyll.

A noteworthy new departure occurred during the St. Petersburg Congress of 1884, when LEOPOLD NICOTRA of Messina asked the Congress to do something, on a basis of international coöperation, towards studying important lacunae with which, according to him, individuals no longer could deal. NICOTRA also made the far-reaching suggestion that all national botanical societies should be united into one international botanical society. The time did not yet seem ripe for such endeavours, for the report says: "Personne ne demandant la parole on

résout de publier les propositions de Monsieur NICOTRA . . ."

In 1885, the 18th Congress met again in Belgium, this time in Antwerp which was developing as an international centre of trade and shipping. It was also the first time that the programme of one of our congresses included many reports and discussions on tropical applied botany, particularly with reference to the Belgian Congo. Another innovation was the *Rapports Préliminaires* issued and distributed before the Congress by CHARLES DE BOSCHERE on the major subjects to be discussed during the Congress. These included discussions on "Le Rôle et l'Organisation des Laboratoires de Botanique" by LÉO ERRERA and E. LAURENT. Many international congresses to-day issue advance reports of the major points to be discussed during the congress, sending these out a good time before a congress is to be held in order that those who attend the congress will come well briefed. With the exception of the *Synopsis of Proposals*, which the International Nomenclature Commission distributes before each of our congresses, I believe that the Antwerp Congress of 1885 was the only international botanical congress which sent out advance reports and discussions on a large scale. The Antwerp Congress also was the last congress which ÉDOUARD MORREN attended, a short time before he passed away. Successful as the Congress was, it was the last of the series of mixed horticultural-botanical congresses. An era had come to an end and, from then on, the international botanical and horticultural congresses developed each along their own lines.

The Madrid Congress which was announced with much enthusiasm for 1886 did not materialize. The 19th Botanical Congress, which was deeply concerned with botanical cartography, met in Paris in 1889; and we may say that the first modern international botanical congress, the 20th, was organized in Genoa in 1892.

This Congress was held on the occasion of the opening of the new botanical laboratory which Sir THOMAS HANBURY had given to the Uni-

versity of Genoa and in connection with the festivities commemorating the quatercentenary of the discovery of America. PENZIG was president and many, who were still with us only a few years ago, attended. Amongst them was the great Russian botanist, J. BORODIN, an honorary vice-president, who opened one of the sessions with the following words:—

“Il fut un temps où l'on n'avait rien raison de dire 'ex oriente lux'.—Les choses sont changées, les faibles lumières qui nous viennent de l'orient ne sont que les reflets de l'immense brasier scientifique, allumé à l'occident. . . avec la modestie qui lui convient et avec une gratitude sincère l'orient s'incline devant le brasier de l'occident. Le disciple salue respectueusement son maître . . .”

Though the Congress had been held at the quatercentenary of the discovery of America, few American botanists attended. Amongst those who were present was UNDERWOOD, who had come to invite European colleagues to the international botanical congress which had been announced, well in advance, for 1893, on the occasion of the Chicago World's Fair. The Congress was well and widely publicized, but when it was held in Madison in Wisconsin under the presidency of Professor ARTHUR, no foreign visitors were present. This was due chiefly to the fact that the Congress was being held late in the year and that it had been preceded by a great many other international (particularly horticultural) activities in Chicago, during the previous months. The “Cosmopolitan Horticultural Society,” established during those horticultural meetings in Chicago, to promote correspondence, exchanges of seeds, books and the extension of fellowship between the horticulturists of the world, seems to have shared the short life of most “world-fair-born” international associations.

A Congress which called itself the “Premier Congrès International de Botanique,” but which was, at most, the last international botanical congress of the century, convened in Paris in October 1900, *in modo gallico*, on the occasion of a world exhibit. It had been well organized by Professor PERROT. BRIQUET, who had been

made Rapporteur Général for nomenclature (a position which O. KUNTZE had tried very hard to secure since the first announcement of the congress in 1895), took for the first time a leading part in nomenclature deliberations. Of the general addresses, HUGO DE VRIES' “Variabilité et Mutabilité” attracted wide attention.

Many discussions on the standardization or stabilization of research methods and a number of resolutions were passed. Amongst these we may mention one calling for the unification of botanical and zoological nomenclature, one dealing with the standardization of plant geographical nomenclature and one concerning the exchange of herbarium material. Another resolution, passed after considerable discussion, called for the establishment of a journal for the publication of new, taxonomic units. It was decided that HUA should edit this journal. For a number of reasons, the project did not materialize, but the scheme resulted later in the *Index Botanique Universel* published between 1902 and 1906 at the Herbarium Boissier, under BEAUVERD's editorship.

The Executive Commission of the Paris Congress also appointed itself a permanent commission of the International Botanical Congresses, and a decision to hold the congresses in the future once every five years, the usual period for large, international scientific congresses, at a time when travel was slow and the majority of scientists lived and met in Western Europe, was made. To-day most large, international scientific congresses meet once every three or four years, at least when conditions permit, and often alternate between Europe and a country outside of Europe.

The 22nd International Botanical Congress met in Vienna in 1905. The great Donau monarchy united through enlightened statesmen such as Count TAUFFE, was at the height of its glory. The arts and sciences flourished and the Austrian, Hungarian, and Czech botanists, inspired and guided by KERNER and his son-in-law VON WETTSTEIN, organized a congress, the reports of which make nostalgic reading to those of us who have had the opportunity of working in

Austria. VON WETTSTEIN and WIESNER were presidents and ZAHLBRUCKNER was secretary. It was, I think, the first time that there was a Ladies' Committee to arrange for a special programme for the wives of the visiting botanists. Before and after the Congress, there were very extensive excursions for which a special guide book had been prepared. There was also an elaborate exhibit, organized by the Congress Committee in coöperation with the newly established *Association Internationale des Botanistes* which also published the "Résultats scientifiques" of the Congress, while the report of the meetings and the nomenclature deliberations were published by the Congress Committee.

In connection with the Vienna Congress, mention should be made of DÖRFLEDER, one of the active members of the organizing committee. Through his exsiccata, his Adressbücher, and *Dörfleria*, he played a great rôle in international botany.

Dr. O. KUNTZE, in spite of his abilities now a rather pathetic figure, was allowed to read a protest against the set-up of the nomenclature commission and its programme of work and to distribute pamphlets outlining his particular views.

Our 23rd Congress met in May 1910 in Brussels. DURAND and DE WILDEMAN were the secretaries. There were 5 sections. It was the first time that several guests from the Orient were present. Amongst them was HAYATA who reported on his work on the Flora of Formosa. Much time was given to the discussion of nature protection (a subject not much discussed before at our congresses), plant geographical mapping and terminology, photography and botany, the arrangement of herbaria, etc.

Speaking on the work of international botanical congresses, DE WILDEMAN presented the following concise philosophy of international botany: "La plus haute représentation des intérêts communs de tous les travailleurs d'une même science consiste à prendre des mesures pour l'organisation du travail. Le Congrès est entré dans cette voie en arrêtant son code de

règles pour la nomenclature. Pourquoi arrêter en si bonne voie et ne pas concentrer toutes les règles et toutes les ententes relatives à l'organisation du travail dans un code unique divisé en autant de parties que de branches d'organisation." With OTLET, the pioneer of international cooperation in bibliographical work, he subsequently proposed "Un Code de Règles pour la Documentation de la Botanique."

After the Congress there were several excursions of which those to the Ardennes and maritime region attracted many.

It is of interest to note that ZAHLBRUCKNER presented a formal report on the Vienna Congress of 1905—the only time, as far as I know, that this was done. It had, without a doubt, something to do with the animosity caused between certain of those concerned with the Paris, Vienna and Brussels Congresses, on the one hand, and the Council of the newly established *Association Internationale des Botanistes*, which considered itself the mother organization of the international botanical congresses, on the other hand.

At the Brussels Congress we note, for the first time, commercial exhibits such as that of Messrs. Zeiss of Jena.

Amongst the resolutions passed were certain calling for international interference in local affairs. Those in charge of the Messina Herbarium presented a motion which called for unification of certain Italian collections, while another motion advised the city of Antwerp, in connection with its projected Jardin Botanique et Musée Colonial. Those familiar with the history of modern international scientific congresses will know of many other cases where congresses passed resolutions in an effort to influence regional affairs, but resolutions of this type are very rare in the history of our international botanical congresses. I think that this is just as well; an international scientific congress should be concerned with international problems—national or local problems, urgent as they may be, belong in the hands of such organizations as national research councils, biological councils, etc.

ROYAUME DE BELGIQUE. — MINISTÈRE DE L'INTÉRIEUR.

BULLETIN

DE

CONGRÈS INTERNATIONAL D'HORTICULTURE

QUI A ÉTÉ RÉUNI À BRUXELLES,

LES 24, 25 et 26 Avril 1884.

SOUS LES AUSPICES DE LA

Fédération des Sociétés d'Horticulture de Belgique,

ET CONCURRENCE AVEC

L'EXPOSITION UNIVERSELLE D'HORTICULTURE,

ORGANISÉE PAR LA SOCIÉTÉ ROYALE DE FLORE.



GAND.

IMPRIMERIE ET LITHOGRAPHIE DE C. ANNOOT-BRUCKMAN.

1884.

Title page of the Proceedings of the first of our international plant science congresses, cf. p. 42.



Charles-Jacques-Édouard Morren

Charles-Jacques-Édouard Morren (1833—1886), Director of the Botanical Institute of the University of Liège, founder of our international plant science congresses, cf. p. 43.

LOIS

DE LA

NOMENCLATURE BOTANIQUE

ADOPTÉES PAR

LE CONGRÈS INTERNATIONAL DE BOTANIQUE

TENU À PARIS EN AOÛT 1867

SUIVIES D'UNE

DEUXIÈME ÉDITION

DE L'INTRODUCTION HISTORIQUE ET DU COMMENTAIRE

QUI ACCOMPAGNERAIT LA RÉDACTION PRÉPARATOIRE PRÉSENTÉE AU CONGRÈS

PAR

M. ALPH. DE CANDOLLE

Éditeur et en partie auteur du
*Prodromus systematis naturalis regni vegetabilis.*GENÈVE ET BALE
H. GEORG, LIBRAIRE-ÉDITEURPARIS
J.-B. BAILLIÈRE ET FILS

1867

Title page of the first edition of the official rules of botanical nomenclature, the Paris Code or Candolle Lois, as adopted by the Paris Congress of 1867, cf. p. 45.

2. M. CH. MARTENS, Prof. de Botanique à *Montpellier*, propose au Congrès de mettre à l'ordre du jour la question suivante:

Influence de l'échauffement du sol par les rayons solaires sur la végétation et la distribution géographique des végétaux.

3. M. CH. LEMAIRE à *Gand*, Rédacteur de l'*Illustration horticole*, annonce un discours contenant:

"Critiques raisonnées et réfutation sur la théorie des boyaux polliniques."

4. M. JEAN PASSERINI, Prof. de Botanique à *Parma*, se propose de discuter:

1. Sur l'émission de l'acide carbonique par les racines des plantes et sur la décomposition du même acide par les parties vertes.

2. Sur la fonction des stomates.

5. M. le Prof. JULIUS SACHS de *Bonn*, traitera le sujet suivant:

Ueber die Wichtigkeit phytometrischer Bestimmungen für die Physiologie, Geographie und Cultur der Pflanzen, und über die Wichtigkeit der dabei zu befolgenden Methoden.

6. M. le Prof. F. COEX de *Breslau*, vient d'indiquer comme questions convenables pour la discussion du Congrès:

1. L'influence que la lumière exerce sur les mouvements des plantes.

2. Les métamorphoses que les ravages de certains insectes produisent dans l'évolution des cellules des plantes attaquées.

7. M. CHATIN, Prof. de Botanique à l'école impériale de Pharmacie à *Paris*, a remis les questions suivantes comme élément de quelques discussions, qu'il ouvrira par un exposé sommaire de ses recherches sur ces sujets:

1. Des caractères anatomiques pour la classification des végétaux.

2. Structure et fonctions du tissu de l'anthère.

3. Du sucre dans les tissus des plantes.

8. M. F. MÜLLER, Président de la Société Royale Linnéenne à *Braszels*, se propose de donner:

Lecture d'une notice sur le genre *Cuscuta*.

et il annonce en même temps un travail sur les plantes de plein air sous le climat de la Hollande et de la Belgique.

A page from the preliminary programme, issued prior to the Amsterdam Congress of 1865, with the names of the principal members who intended to attend, and the subjects they proposed to discuss, cf. p. 44.



A view of the large exhibit in the Orangerie at Schönbrunn organized by the executive committee of the Vienna Congress of 1905 in coöperation with the Association Int. des Botanistes, cf. p. 47.



Participants in the Vienna Nomenclature Discussions, June 16, 1905.

Front row, from left to right: J. Arboist, Th. Durand, H. Schinz, J. N. F. Wille, E. Hackel, B. Robinson, E. Bonnet, J. Urban, W. Trelease, P. Magnus, C. F. O. Nordstedt, Ch. Flahault, A. B. Rendle, J. Briquet, F. Fedde, H. Harms, G. Wolkens, H. Knoche. — Second row: G. Hegi, Miss Perkins, O. Warburg, J. Borodin, X. Gillot, L. Lutz, E. Perrot, L. Wittmack, G. F. Atkinson, A. Engler, P. Ascherson, E. Warming, C. Mez, A. de Jacewski, A. v. Hayek, F. Graf v. Schwerin, L. Diels, E. Gilg, A. Voigt. — Third row: C. Schröter, L. Errera, J. C. Arthur, A. v. Degen, H. Hua, P. Chenevard, E. Wilczek, C. H. Ostenfeld, F. Cavillier. — Fourth row: — G. Beauverd, F. Filarszky, M. de Vilmorin, R. v. Wettstein, Ch. R. Barnes, K. Fritsch, A. Rehder, J. H. Barnhart, H. Lindberg, D. Prain, R. Maire, C. Brick, E. Zacharias, G. Hochreutiner, H. Hallier, C. Domin, O. Mattiolo, N. L. Britton. — Back row: E. v. Halácsy, E. De Wildeman, G. v. Beck, E. Burnat, F. V. Coville, B. Schorler, O. Drude, J. W. C. Goethart, L. M. Underwood, C. Shear, O. Penzig.

CONGRÈS INTERNATIONAL
DE BOTANIQUE.1^{re} Session: Paris 1900.
2^e Session: Vienne 1905.5^{me} Circulaire
de laCommission permanente
des
Congrès internationaux
de Botaniqueconcernant la participation du Bu-
reau permanent à la préparation
du 2^{me} Congrès international de
Botanique à Vienne 1905.

A.

5. Zirkular*)
derPermanenzkommission
der
internationalen
botanischen Kongressebetreffend die Teilnahme des Per-
manenten Büros an den Vorberei-
tungen zum II. internationalen bot-
anischen Kongress in Wien 1905.INTERNATIONAL CONGRESS
OF BOTANY.1st Session: Paris 1900.
2nd Session: Vienna 1905.5th Circular*)
of thepermanent Committee
of the
international Congress
of Botanyreferring to the participation of the
permanent Board in the prepar-
atory steps for the 2nd international
Congress of Botany at Vienna 1905.

Dans sa Séance du mardi 9 octobre, le Congrès de Paris 1900, a décidé à l'unanimité*) de priver le Bureau du Congrès de rester en fonctions jusqu'à la nomination du Bureau du Congrès de 1905, constituant ainsi une Commission permanente chargée de se mettre en rapport avec les organisateurs de la Réunion de Vienne en 1905, dans le but de prendre en compte les mesures nécessaires pour la complète réussite du II^e Congrès périodique international de Botanique.

La Commission d'organisation de ce dernier est définitivement constituée depuis le 1^{er} janvier 1903 et le Congrès de Vienne s'annonce sous les meilleurs auspices.

*) Actes du Congrès international de Botanique 1900, pp. 453-455.

In seiner Sitzung am Dienstag den 9. Oktober hat der Pariser Kongress von 1900 einstimmig beschlossen: 1. das Kongressbüro zu bitteln, bis zur Ernennung des Kongressbüros von 1905 die Tätig-
keit des Kongressbüros von 1900 zu beibehalten und auf diese Weise eine Permanenzkommission zu bilden, welche mit der Aufgabe betraut ist, sich mit den Veran- staltern der Zusammenkunft in Wien 1905 ins Einvernehmen zu setzen, zu dem Zwecke, gemein- schaftlich die nötigen Vorkehrun- gen zum vollständigen Gelingen des II. periodischen internationalen botanischen Kongresses zu treffen.)

Das Organisationsbüro dieses letzteren besteht seit 1. Januar 1903 und der Wiener Kongress bereitet sich zu demselben.

*) Die Organisation dieses Kongresses aus dem französischen ins Deutsche und Engli- sche erfolgte mit Zustimmung der Pariser Kommission durch die Wiener Kommissi- on. Actes du Congrès international de Botanique 1900, pp. 453-455.

First page of one of the three language circulars (No. 5, Oct. 1903) distributed by the 1900/1905 permanent commission of the international botanical congresses, i. e., the executive committee of the Paris Congress of 1900, cf. p. 47.

D^r. OTTO KUNTZE

PROTEST

GEGEN DEN VOLLMACHTSWIDRIG ARRANGIERTEN
und wegen vieler Unregelmäßigkeiten
INKOMPETENTEN NOMENKLATUR-KONGRESS

auf dem internationalen

BOTANIKER-KONGRESS IN WIEN
nebst Kritik der dürftigen Resultate
der internationalen Kommission

UND VORSCHLAG

ZU EINEM BALDIGEN KOMPETENTEN KONGRESS



San Remo (Villa Girola) Italien
IN KOMMISSION BEI ARTHUR FELIX
LEIPZIG
1905

Cover page of a memorandum, in which O. Kuntze outlined his views on botanical nomenclature and the organization of the international commission for botanical nomenclature, distributed during the Vienna Congress of 1905, cf. p. 48.

Had the First World War not interfered, the next international botanical congress would have been held in London, in 1915. At a meeting of the British organizing commission in the spring of 1915, it was decided to postpone the congress until 1920. At that time, the atmosphere was so troubled that the British preferred to arrange one of their Imperial Botanical Congresses, and it was not until August 1926 that our Congress convened again and for the first time on the other side of the Atlantic, at hospitable Cornell University in Ithaca, N. Y.

This 24th Congress was the first one which was called a congress of "the plant sciences." Dr. LIBERTY H. BAILEY presided over a large gathering of American and overseas scientists representing more branches of the plant sciences than had ever before been brought together. Speaking about the Ithaca Congress, a friend said, the other day, "I never went to a Congress where there was so much rain, yet it remains the nicest Congress I ever attended." As there is now much talk about having one of the next international botanical congresses again, after more than 25 years, on the other side of the Atlantic, we should say no more about the Cornell Congress for this might be considered unfair influencing of the voters.

The postponed English Congress met in 1930 under the presidency of Professor SEWARD, whose garden party at Downing College is fondly remembered by many of those present today. As in Ithaca, many of the members were lodged in University College rooms and greatly enjoyed their unique atmosphere. Before the Congress, many went to London where there was a reception at the Imperial Institute and open house at the Linnean Society. The British Museum of Natural History received a large group of members during the latter part of August, after the Congress.

The official programme of the Congress included an organ recital and the awarding of honorary degrees by the University of Cambridge. There were 8 sections. Amongst the subjects discussed we may mention: the classification and nomenclature of vegetation, the

mapping of vegetation, the species concept, floral organization, the very fine palaeobotanical programme, and many papers dealing with the international aspects of plant pathology. There were excursions to Kew, Rothamsted, John Innes, etc., and a plant geographical excursion to the English beechwoods and the Southern chalk country.

Much interest was aroused by HALL's proposal for an International Bureau of Plant Taxonomic Herbarium Administration, a forerunner to the present plans for an International Association of Plant Taxonomists.

Resolutions of the Congress were concerned with the nomenclature of microorganisms, the need for a uniform geobotanical map of Europe, the terminology of plant synecology, phytopathological needs, plant viruses, urgent taxonomic needs, etc. The Commission for Urgent Taxonomic Needs, some time after the Congress, issued an international botanical address book, under the editorship of one of the energetic congress secretaries, T. F. CHIFFS, who unfortunately passed away on June 28, 1931, at the age of 45. BRIQUET acted for the last time as Rapporteur Général for Nomenclature, and after the Congress he edited the third edition of our International Rules of Botanical Nomenclature. The Congress, as you all know, had been instrumental in making peace in Nomenclature between the Old World and the New. The original American Proposal embodying the American Code, of 1904, had been rejected by the Congress of Vienna in 1905. After the First World War, a compromise was prepared by some British and American botanists, this was presented in the 1930 Synopsis and accepted. It introduced the "Type-method" into official botanical nomenclature.

The 1935 International Botanical Congress, organized by the late Professor WENT and Dr. SIRKS, met in Amsterdam in September, under the presidency of Professor SCHOUTE, in the buildings of the East Indies Institute. Amongst the general papers LLOYD's on *Utricularia* aroused much interest. An evening of botanical humour and cartoons, projected from lantern

slides, as well as songs arranged by Professor WESTERDIJK, in which the distinguished auditorium eagerly participated, was something none of the 25 previous congresses had ever seen or heard.

There were several excursions amongst which one to the new Zuiderzee polders and one through the harbour, are still fondly remembered.

Since the Gesellschaft Deutscher Naturforscher made its trip through the harbour of Hamburg in 1930, excursions on steamers have been pleasant and favourite interruptions of congress sessions, and no less an authority than ABDERHALDEN has suggested that it would be useful to hold entire international congresses on board large steamers.

Amongst the resolutions passed at the Amsterdam Congress, we may mention the first which made the Botanical Section of the International Union of Biological Sciences the official interim organization of the international botanical congresses, one calling for an index of the herbaria of the world, one calling for an international dictionary of botanical terminology, and several regarding the standardization of terminology. The resolutions were executed or publicized, as well as pre- and post-war circumstances permitted. The *Index Herbariorum* is now in active preparation. It is to be regretted, however, that no editor has been found, as yet, for the international dictionary of botanical terminology.

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In addition to the official international botanical congresses which we have just reviewed, there were, of course, many other early congresses concerned with botany. It has already been related how the International Horticultural Congresses developed along independent lines after 1883. Another group of early congresses, which attracted many botanists and exercised much influence, were the International Conferences on Plant Breeding and Hybridization (1: London, 1899; 2: New York, 1902; 3: London, 1906). They were the forerunners of the International Genetical Congresses.

Before the turn of the century, there already were many international congresses dealing with the applied plant sciences, such as agriculture, viticulture, pomology, sericulture, forestry, etc.

It was, of course, only natural that, with the increase in the number of branches of the plant sciences, the growing number of biologists and the improvement of travel facilities, there should arise all kinds of special international botanical congresses, conferences, excursions, associations, etc. Some of these, as the series of Alpine Garden Congresses of which the first one was held in 1904, were short-lived. Others, as the International Congresses for Horticulture have developed steadily, drawing a good number of botanists to each of their meetings.

At present, we have about 200 international congresses, conferences, associations, in the plant sciences, ranging from the International Cocoa Conference to the International Lucerne Trial, from the International Association of Wood Anatomists to the International Commission for Agricultural Chemistry, while UNESCO, FAO and the International Council of Scientific Unions endeavour to guide, coordinate and stimulate further activities.

Phytopathologists, strange to say, formerly were more internationally minded than they are to-day. Before the turn of the century, we already had a series of International Rust Conferences and an active International Phytopathological Commission. Particularly inspiring, though often little understood, even in his own country, are the views expressed by the great Swedish pathologist JAKOB ERIKSSON, whose essay of 1891 is one of the great classics in the history of international scientific co-operation.

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After attending the Genoa Congress of 1892, UNDERWOOD wrote in the *Botanical Gazette*: "Were we called upon to suggest any changes of program or method for a gathering of botanists even more successful than this, we would say (1) reduce the number of papers read, (2) introduce

a few topics for discussion that would command universal attention, (3) increase the facilities for personal and social intercourse among the members. The grand object of such a meeting is to facilitate the personal acquaintance of members and the discussion of questions of general interest, rather than stiff formality and the presentation and discussion of local questions. Every effort to secure these two ends should be most carefully studied."

Now, more than fifty years later, approximately the same remarks are being expressed after each of our current, large international congresses. It may be well, therefore, to consider the aims and purposes of our international plant science congresses briefly.

In the first place, they enable the plant scientist, young or old, to present a personal report to his colleagues about his current work or his views. I think that this is still always their most important function. The programmes of some of our past congresses consist of nothing but an unrelated series of papers. All modern congresses announce in advance which topics will be given particular attention. In addition to the symposia, which this useful procedure creates, we need perhaps more informal round-table conferences on practical needs or methods of policy. It is often said, these days, that the number of individual papers to be presented at a congress should be drastically limited. I do not think that this view is correct. No one has to go to a session in which he is not interested, and I strongly feel that it will be better to have more sections than a totalitarian reduction in number of individual papers. Let us not forget that "words may still always refresh, exhort and even set hearts afire . . ." On the other hand, the spirit of a well prepared international congress is such that those who take part in it realize that they do not come primarily to report about their personal triumphs or worries but to contribute to the unification of their science.

In the second place, our congresses enable us to meet colleagues whom we can otherwise know only by the exchange of letters or reprints. Some generations ago the majority of scientists

had to be satisfied with exchanging reprints, letters, and small photographs with their foreign correspondents. To-day, at our international congresses, most of us are able to meet our foreign colleagues and to talk with them.

In this century of wars, international congresses serve also to re-establish scientific relations between the sons and daughters of the warring nations. Yet, we will all agree that those few who, by their free will, have misused their culture in schemes of world conquest, should have the good taste to stay away from our meetings.

Most botanists, as true plantmen, love the earth and hate the world. Only when the need for coöperation and standardization becomes desparately high, will we use our congresses as legislative bodies. Nevertheless, they have served well in this third capacity, as shown by the work of the International Nomenclature Commission, the effects of many recent resolutions calling for the standardization of terminology, etc.

Since the Paris Congress of 1900, our congresses have formulated resolutions calling for many things, ranging from the reduction of postal rates on herbarium specimens to the protection of the flora of Africa, and from the unification of the colours used in plant geographical maps to the compilation of a dictionary of botanical terminology. These things can occasionally be accomplished by individuals; but, as the science of plants progresses, its problems become more involved and, in each generation, there are more things which individuals no longer can accomplish. It is clear that when a large number of resolutions are passed, there should be some organization responsible for their execution on an international cooperative basis.

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Even when the Belgian Federation held itself responsible for the organisation of the early congresses, our congresses were rather independent manifestations. Before the First World War, Lotsy's "Association Internationale des

Botanistes" went to considerable efforts to establish approximately the same type of relationship between the Association and the International Botanical Congresses, as we now find between such extremely effective international organizations as the International Union of Chemistry and the International Chemical Congresses.

LORTSY's Association Internationale des Botanistes was the only large and truly international society of plant scientists with a personal membership, which we ever have had. It held itself to a large extent responsible for the international botanical congresses and the execution of their resolutions; it also organized annual meetings of its council or Assemblées which were open to its entire membership. Amongst its chief activities was the reorganization and editing, on a strictly international basis, of the *Botanisches Centralblatt*. It also sponsored such organizations as WESTERDIJK's International Collection of Fungus Cultures, and several commissions were active with special projects when the war of 1914-1918, and perhaps also a change of LORTSY's interests, terminated the organization.

As farsighted as LORTSY's scheme may have been, it often overlooked the fact, to which I have referred already, that botanists are not chemists; they are plantsmen and tend to like their flowers better than their colleagues. I think we all agree that it is better for the international botanical congresses to remain fairly independent organizations and for the interim organization to concern itself only with the execution of the resolutions of the congresses.¹

Although I have spoken at such length about congress resolutions, I still might mention two, which, some fifty years ago, caused considerable interest in the botanical world even though the projects called for never materialized: (1) the establishment of an international botanical station at Palermo and (2) BUSCALIONI's project for an international botanical institute in the

Amazon valley — a kind of forerunner of UNESCO's Amazon project.

*

In discussing international relations and cooperation in the plant sciences, it is easy to agree with CARL AUGUST when, instead of going to a command audience with Napoleon, he disappeared in the Dresden Botanical Garden: "Als ich ringsum so viel Untreue, Verrath und Betrug sahe, da bin ich an der Menschheit verzweifelt und in meiner Verzweiflung hat mich allein die alte Liebe zur Natur aufrecht erhalten und ich habe mich in sie versenkt. Und da mich die Menschen anekelten, bin ich zu den Pflanzen gegangen und habe sie studiert und habe mit den Blumen verkehrt,—und die Blumen haben mich nicht betrogen."

At one time, we were chiefly hunters or growers of rare and unusual plants. To-day we are no longer primarily concerned with these activities but instead with a critical and systematic inventory of the world's plant resources, on the one hand, and with the entire science of biology, its huge implications into human welfare, and with its connection with other branches of the natural sciences, on the other hand. From our isolated valley or conservatory, we have entered a field which is directly concerned with the interests and future of the world at large. In comparison with workers in many other branches of science, we remain in the happy position that in serving the progress of biology—be it general or systematic biology—we will ultimately serve applied biology and mankind.

Yet, there are many new developments in pure biology—ranging from genetics to plant geography and from plant physiology to mycology—which have not yet found the applications which they obviously merit. This is often due to the effects of overspecialization as a result of which a worker in some applied field is not able to grasp the implications of work done, for instance, in pure plant physiology; but in a great many cases of this type, a wider international outlook may be a great stimulus as new advances in pure biology in one part of the

¹ This of course means also that if a congress could not be held as planned, the interim organization would have the duty of arranging for a substitute congress.

world are often of particular interest for applied biology in an entirely different region.

*

What we may call international interaction—to contrast it with formally organized international coöperation—is sometimes overlooked in considering international scientific activities. I find myself at some fault for having written rather lengthy papers on international scientific coöperation in biology without stressing the various aspects of simple international interaction. It may be of interest to list a few examples.

The most striking advance made in agriculture during the past fifty years is the improvement of agricultural commodities through breeding and hybridization. Application of the fundamental laws of MENDEL was mainly responsible for this tremendous achievement. In the field of plant breeding, nations and even continents have no boundaries; to the marked benefit of civilization as a whole. On the other hand, international law and ethics ask for some regulation and protection of breeders' results. A convention to formulate this has been considered from time to time and will, without a doubt, be held before long under the auspices of the FAO.

It is desirable, in the development of improved crops and particularly in breeding for disease resistance, to have specimens collected in widely scattered areas all over the world which might in themselves carry resistance and so contribute valuable material for investigations in breeding for resistance. Until a short time ago, Russia supplied many important grasses. Potatoes and other solanaceous plants have been secured from South America. Generally speaking, the collectors sent out by the various departments of agriculture receive assistance from the departments of countries they visit in keeping with the unwritten laws of unhampered international exchange.

A fundamental advance in one field in one country is bound to be of importance in another elsewhere. You will recall that boron was described as an essential element by British workers. This has helped enormously in combating several difficulties, as they occur, from time to time, in the United States. Again, if we may go back a few years, the work on the Dutch Elm Disease in Holland and Germany was of tremendous importance in the United States when that disease appeared there, having apparently been transported across the ocean on veneer logs. Going back still further, we see that European work on wheat

rust and potato blight have been very important indeed for pathologists in the U.S.A.

The natural sciences, indeed, are a particularly fruitful field for international collaboration, because, as one of the resolutions of the first U. N. Conference on Food and Agriculture has said: "They are themselves international and universally accepted." "There is already a good deal of collaboration," the resolution continued, "but much more could be done . . ."

Let us now, therefore, briefly consider the theoretical aims of closer, international scientific coöperation:

- (1) The exchange of information, whether scientific, professional or practical, in such a way that it will be available to anyone who can profit by it.
- (2) The attainment of objectives which individuals or scientists of a single institution or nation cannot accomplish. These may range from research projects on the effect of radiation on the vegetation to such publications as the *Flora Malesiana* or the *Index Herbariorum*, and from the compilation of the International Rules of Botanical Nomenclature to a preparation of a polyglot standardized dictionary of terms used in wood anatomy.
- (3) The formation, to say it with simple words, of a "Quaker spirit" in science which may, at least at times, offset the evils of human international politics and contribute towards a commonwealth of man.

In practice, these aims may be realized in a variety of ways, all of great interest from our point of view:

- (1) by various forms of coöperative research,
- (2) by international conferences and congresses,
- (3) through international commissions and committees responsible for the solution of specific problems,
- (4) by personal contacts, visits and correspondence,
- (5) by the exchange of research materials, specimens, literature, etc., or the gifts of such materials to institutions in war-damaged regions,
- (6) by the exchange of professors, research workers and students,
- (7) by various publications, ranging from scientific journals to news journals, from abstracting journals to international directories and censuses of current research, from Indices to a series of Generic Floras so much needed for the unification of botanical science.

In biology (which apart from a few fashionable subjects, is an understaffed and underfinanced branch of the sciences), there is an endless number of projects which cry out for close international coöperation along one or several of the seven approaches which I have outlined above.

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Generally speaking and considering all aspects from the point of view of pure science as well as that of human welfare, I would say that we now have enough international congresses, meetings, and symposia; according to some, we also have a sufficient number of journals, and there exists full opportunity for international exchanges of various types. But, as I see it, we need more critical studies (with exact figures, not general essays) on what closer international coöperation may do in certain fields; how it can be accomplished; how much it will cost; how long it will take; how the results should be published if necessary; how and where the work should be managed.

Then (when it has been established that, with certain funds and within a certain time, close international coöperation may well yield results which individuals cannot accomplish), a commission of limited scope should be established within the framework of the large existing organizations coöperating with UNESCO or FAO, under the chairmanship of an energetic and idealistic, yet practical, scientist who will consider the appointment not primarily an honour but a duty. Far away indeed is the period of botany when ROUSSEAU called it "la véritable occupation d'un corps ambulant et d'un esprit paresseux . . .".

For certain subjects, we need international research centres, but botanists, unfortunately, seem nearly always to meet with the same response as MARIE STOPES when she applied to ANDREW CARNEGIE for assistance towards an international palaeontological institute, to be established in London: "In New York," it is related, "she met CARNEGIE, who invited her to his palatial home, and she found him very

different from the hard old man rumour had described him as being. He gave her tea in tête-à-tête comfort, and though he refused an endowment for palaeontological research which she asked him for, he received the request with such humour and such personal charm that she went away feeling she had gained a great deal. And perhaps she had, for this wise old man said to her: 'You are far too clever, my dear, to be wasting your time over fossils; things that live matter more. If you had come to me with a proposition that would help the peace of the world, I would not have given you a quarter of a million, I would have given you a million, and gladly. Take my advice, and do not waste your time over these dead-and-gone things.' The palaeontological enthusiast then pointed out to him that the whole of his wealth rested on the use of coal, and therefore the palaeontological study of its nature and structure must have value, even to him. But he would not see it, and said: 'You are clever enough to make all the millions you want for yourself. We dug coal before you scientists existed, and we can go on digging it without you.' Patting her kindly, he led her downstairs, right down his front steps on to the street in most kindly and fatherly fashion and next day sent her a book of his own, inscribed as follows: 'For relief from severer studies likely to destruct the brain' " (MAUDE, A. 1933: MARIE STOPES, p. 108-109).

Yet, the world of botany needs international institutions or centres to take care of problems with which individuals no longer can deal. In a recent memorandum¹, I told how cryptogamic systematic botany, particularly tropical cryptogamic botany, has reached a confused state where international coöperative action is needed; and I outlined, in detail, how an International Association of Cryptogamic Botanists might cope with these problems.

We also have to give more thought in our international gatherings to the sad fact that there are, on the one hand, a great many fields

¹ The Future of Exotic Cryptogamic Botany (Bryologist 53: 1-9, 1950).

of biology which are being completely neglected at present, while on the other hand, hundreds and hundreds of good biologists are non-productive, due to the fact that they think chiefly in the terms of a limited number of fashionable research projects, research projects on which they cannot work; whereas they could contribute often and valuably to certain neglected fields.

Last but not least, we cannot make the modern, highly specialized biologist, with his limited outlook, more internationally minded unless, as NEEDHAM and HUXLEY understood so well, we stimulate research in and a better understanding of the untrodden borderlands between the humanities and the natural sciences. This is a matter of the utmost importance, and it should be given full consideration by our congresses.

Yet, some of you may say, we must not forget that biology has developed quite well without other international cooperation than the conventional exchange of ideas through publications. The science of biology, indeed, is the result of the work of great individuals and real progress through international coöperation also will almost always be centered around the efforts of single, gifted men, who need the help of a world-wide circle of associates to break a stalemate.

The editor of the "Journal of Botany" once wrote: "The qualities which go to make a good botanist have a curious and profound resemblance to those which go to make a good statesman. Both professions need, above all things, patience, energy, and endurance. In fact, what LINNAEUS himself said about the one profession is equally true of the other: *Botanicus verus desudabit in augendo aramabilem scientiam*. Both professions need a firm grasp of apparently trivial detail; and a preference for the rare (even when it is soberhued) over the commonplace (even when it is conspicuously attractive). Both statesman and botanist must be able to handle other human beings, to inspire their confidence and to justify it. The botanist (like the statesman) must be neither afraid to reach up for what he is seeking, nor ashamed to kneel down for it. And, finally, the statesman (like the botanist) must have that sublime singlemindedness which makes him indifferent to ridicule."

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To all of those taking part in such an effort, international coöperation will mean something different: to some, a way to obtain results otherwise not obtainable, to others becoming acquainted with the somewhat different way of working and thinking of overseas colleagues, this will give a special stimulus; others, on the other hand, will find their drab daily routine more worth while, when it becomes part of a world-wide effort. But there is something else in international scientific relations and coöperation which we tend to forget.

Last year, the second centenary of the birth of GOETHE, there was much said and written about his role in the development of the natural sciences. It seems clear that even if GOETHE had never published anything in science, things would have developed approximately as, in fact, they did. The interesting question to-day, it seems, is not what did GOETHE contribute to science. It is: what did the observation and study of nature contribute to GOETHE? What did it contribute to one of the greatest minds of all times, to a man who influenced and still influences thousands of others, not by his writings on the nature of colour or the morphology of plants, but by his way of teaching the close interrelationships between the humanities and sciences, by the way he taught us that a humanistic attitude and outlook should be the ultimate endeavour of individuals as well as of the nations and mankind, by the way he taught us how the mind shall be our master?

*Denn alle Kraft dringt vorwärts in die Weite,
Zu leben und zu wirken hier und dort;
Dagegen engt und hemmt von jeder Seite
Der Strom der Welt und reist uns mit sich fort.
In diesem innern Sturm und äussern Streite
Vernimmt der Geist ein schwer verstanden Wort:
Von der Gewalt, die alle Wesen bindet,
Befreit der Mensch sich, der sich überwindet.*

We biological research workers, organizers, and teachers must equally realize that the question is not only what the study of nature by more elaborate international coöperation will contribute to biology and human welfare, but also what will the widening and deepening of ex-

perience which stems from the study of nature by closer international coöperation do for us.

It will, I may conclude, assist us greatly in taking our proper place in the world by giving us a better understanding of our rôle in the eternal trinity of man, living and lifeless nature, a proper understanding of which is the only basis for further progress so long as our earth may continue to belong to the living generation.

Professor Dr. F. W. WENT,

California Institute of Technology, Pasadena,
Calif., U.S.A.:

*The Effects of Climate on Plant Growth
and Distribution*

Mr. President, Ladies and Gentlemen, Fellow
Botanists:

It is not only an honor, but also a real pleasure to address a group of such eminent colleagues as I see here before me. It also makes me feel apologetic, for I realize that so much of what I want to discuss has been developed by you, and by our eminent predecessors who are no longer with us, and yet time limitations prevent me from acknowledging each person's contributions. I hope that the international atmosphere in this hall will be sufficient to keep the realization alive that scientists of all nations have contributed towards our concept of climatic control of plant development.

In the course of the last 50 years we have seen develop a strong specialization in the field of botany. Whereas men like SACHS and DARWIN, while contributing research on specialized problems, still considered the plant cover of this planet as their general problem, most of us have restricted even our ultimate aim and are satisfied to see just a special field or facet filling our mental horizon. Yet, as ultimate aim, we should see the converging, instead of the divergence, of all botanical disciplines. To this end we all have to work together, to make each other acquainted with some of the more basic achievements in our particular branches of specialization.

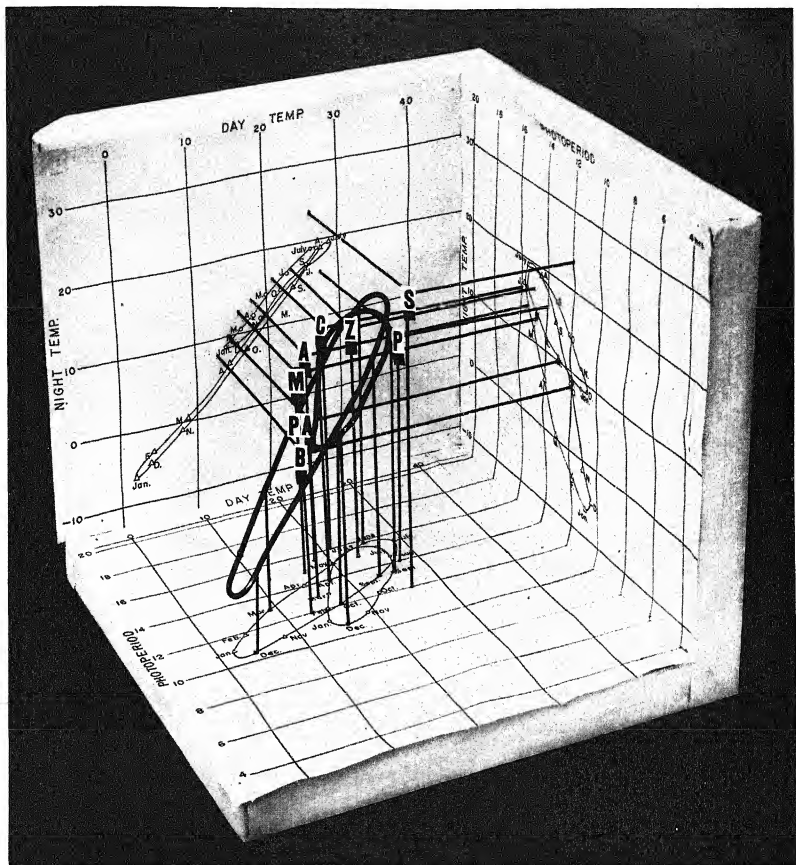
The problem of plant distribution is one in which many botanical disciplines are involved, and in which they should collaborate or even merge.

The occurrence of a certain plant in a given place depends on an almost endless number of factors, which all are equally essential, although not equally decisive for different conditions and plants. A list of essential factors in the occurrence and distribution of the plant should include

- (1) seed dispersal
- (2) presence of soil
- (3) water at the right time
- (4) absence of predators like deer, gophers, snails or insects
- (5) proper control of pests
- (6) relative absence of diseases
- (7) nutrition and soil moisture
- (8) influence of plants on each other through shading, root competition, etc.
- (9) proper climatic conditions for germination, seedling growth, vegetative development, flowering and fruiting.

We know less about the last two sets of factors in connection with plant growth, than about any of the others. This is not so much due to a lack of recognition of the importance of competition and climate, as to a lack of proper experimental facilities. It is only in the last few decennia that microchemical methods have been worked out, enabling us to analyze and identify the minute amounts of chemical excretions, by which for instance *Parthenium argentatum* or *Encelia farinosa* reduce competition by other plants, poisoning them. In the next decennium we can look forward to a rapid development of this new field of Ecology: Biochemical Ecology. I expect that the microchemical study of root secretions will uncover the basis for plant competition, crop rotation and "Bodenmüdigkeit" in a surprisingly large number of instances.

The study of the effects of climate on plant growth and distribution has not only been hampered by a lack of methods, but also by a

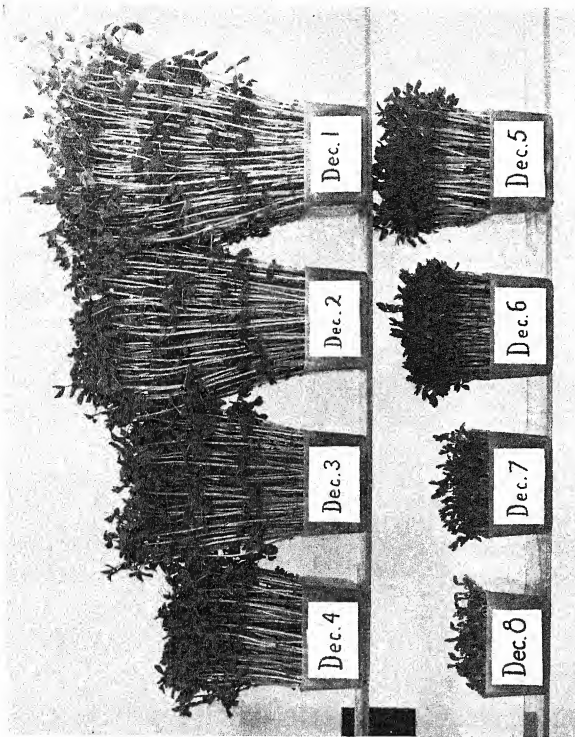


Three-dimensional graph—vertical axis: night temperature; left-to-right axis: day temperature; receding axis: photoperiod.

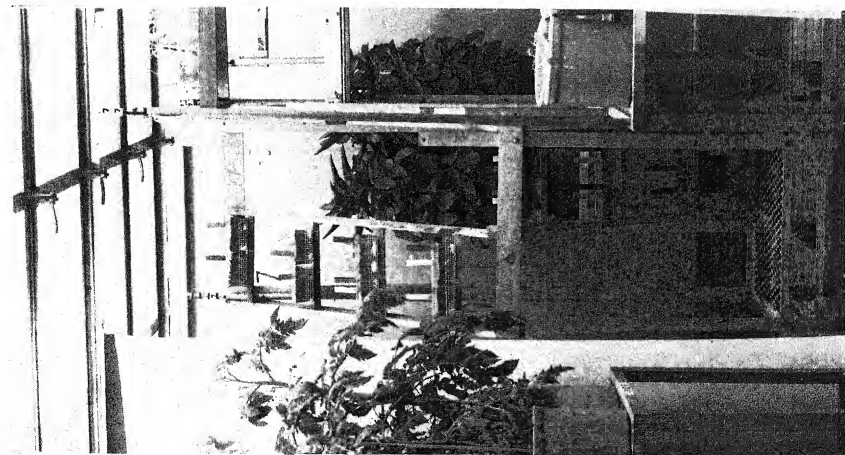
Optimal growing conditions for:

- S = *Saintpaulia*
- Z = *Zinnia*
- B = *Bellis perennis*
- M = *Matthiola*
- PA = *Papaver nudicaule*
- A = *Ageratum*
- C = *Callistephus*.

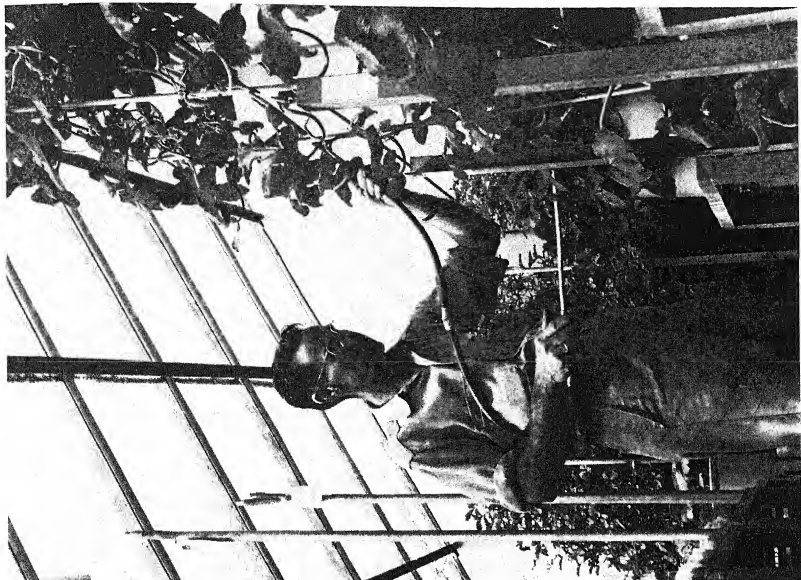
Upper ellipse shows the Pasadena, California, climate throughout a year; lower ellipse gives the Denver, Colorado, climate. See p. 59.



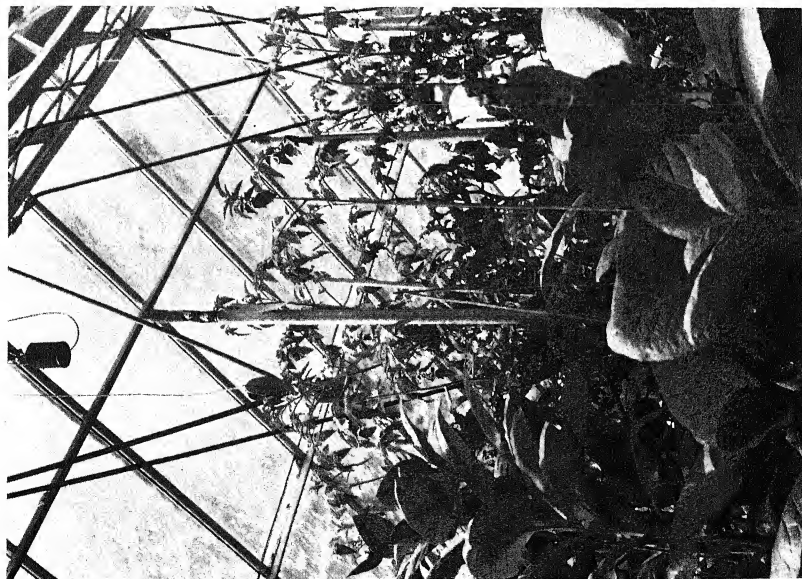
Photograph taken on December 14 of peas planted on the days indicated, and kept in artificial light at 20° C. — California Institute of Technology.



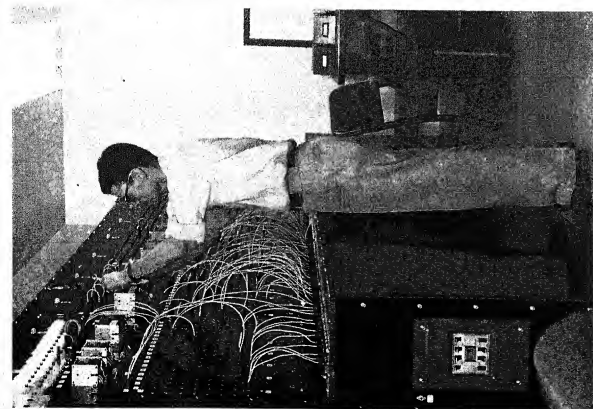
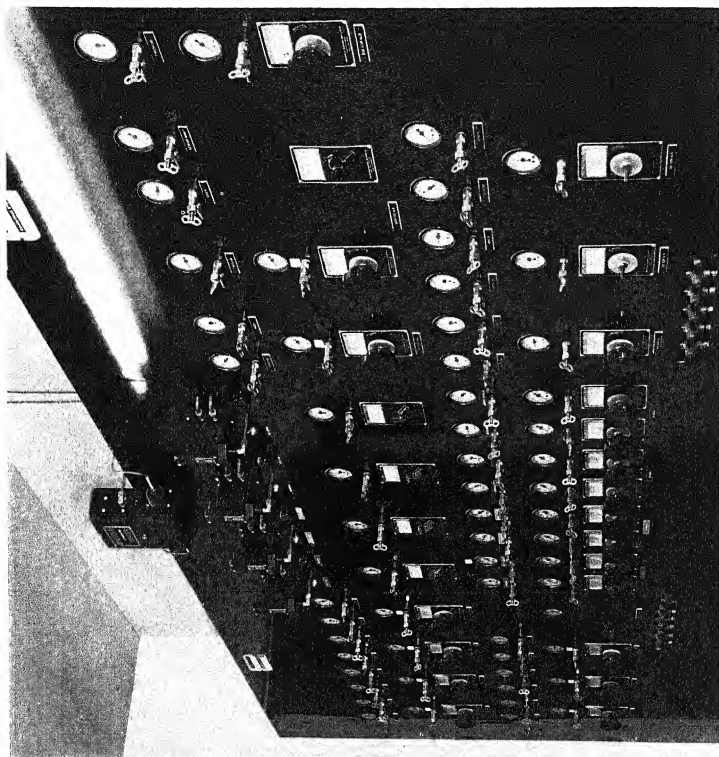
View of artificial light room, in which sections can be partitioned with curtains. Note wheeled trucks on which plants are grown. — California Institute of Technology.



Gardener watering plants in an air-conditioned greenhouse, with water running over glass roof. — California Institute of Technology.



Interior of air-conditioned greenhouse. — California Institute of Technology.



Superintendent adjusting timeclocks in the control room.
— California Institute of Technology.

West side of control room with indicator panel of air-con-
ditioning system. — California Institute of Technology.

good characterization of what "climate" is. Climate is an unpredictable succession of cold and warm days, dry and wet periods, temperature fluctuations throughout day and night, cloudy and sunny weather, various intensities of wind, etc. To make any sense out of this, we have to work with averages, but they are not only abstractions, but also misleading. A yearly rainfall of, for instance, 400 mm may be sufficient for an extensive vegetation cover if evenly distributed over the growing season, but will result in a desert-steppe if concentrated in only a few winter months.

To characterize a climate by average temperatures, we make the same misleading generalization. We realize, of course, that the yearly average temperature is meaningless as far as plant growth is concerned. The magnificent research of BLAAUW and co-workers has shown that in bulbs, such as tulips, hyacinths, onions and daffodils a succession of processes occurs, such as leaf initiation, flower initiation, preparation for stem elongation, actual stem growth and flowering, each of which requires a very different temperature for its completion. These temperatures lie so far apart that many of these bulbs can not develop in any one temperature, if kept constant or even with daily fluctuations. The same thing is true for most deciduous trees from temperate regions: when planted in the tropics at such an altitude, that the average temperature equals the yearly average of their homeland, they usually die within a year.

We can take the seasonal fluctuations in temperature into account, by using monthly or weekly averages. But even then we make two fairly important mistakes: In the first place do these averages differ from year to year: the plants are not subjected to the temperature as occurring on the average of 20-100 years, but as occurring in an actual year, which may differ several degrees from the average. In the second place should we distinguish between day and night temperatures, because very different processes occur in the plant in light and in darkness, and each of these processes has a different

optimal temperature. Thus we see that we *must* take into account both the seasonal and daily fluctuations in temperature, if we want to describe a climate so that it gives a basis for understanding plant distribution.

Another exceedingly important factor in the growth of plants is the photoperiod, or the length of day in relation to night. In contrast with temperature the day length is exceedingly constant from year to year. Its importance in the distribution of plants has been known since the fundamental work of GARNER and ALLARD. More recently it has been pointed out that the effect of photoperiod is not independent of temperature at all.

Other climatic variables, such as rainfall, are less important in the distribution of crop and garden plants, because through irrigation we can control the water supply to plants independently from the rainfall. In deserts averages of rainfall have no meaning at all. Since we know practically nothing at all about the effects of fog and wind of plant growth, we can provisionally exclude them from a schematic summary of the climate of a particular locality.

We come now to the conclusion, that with 3 parameters: day temperature, night temperature and length of day we can describe any climate at any particular time of the year in terms which are of importance for plant growth and plant distribution. These 3 parameters can be plotted along 3 coordinates, and then we can plot the climate of a particular locality in such a 3-dimensional grid. For this we connect the monthly averages by lines, and thus obtain an ellipsoid structure, which indicates the average day temperature, night temperature and photoperiod at any time of the year in a particular location. Within that same grid the climates of other localities can be plotted, and then we suddenly have a means of comparing climates as far as plants are concerned.

We should then know how plants respond to the 3 climatic factors which we have used in our plot of climates. This cannot be done in field experiments, because of the fluctuations in temperature, wind, and other variables. In the

laboratory it can be done, provided a high enough light intensity can be obtained. This is now possible with the newer electric lamps which are available, and in many laboratories rooms with controlled temperature, humidity and artificial light have been installed, Light intensities between 500 and 2000 footcandles (5000–20 000 Lux) are easily obtainable. Yet for most plants this is not quite enough for optimal development. If we want much more light, we are still dependent upon the sun.

To control the temperature, however, in a greenhouse, is a problem which has only rather recently been solved in a satisfactory way. The total radiation of the sun consists of both heat and light radiation in about equal proportion. Most of the light radiation entering a greenhouse is also transformed into heat, partly of evaporation, and partly sensible heat. All this heat has to be removed from the greenhouse again. This can be done by ventilation, by convection, and by radiation. Of these ventilation is the only practical way if good control is desired. But because the specific heat of air is so low, very large volumes of air have to be moved through a greenhouse to remove the heat resulting from the radiation. Per minute enough heat is radiated to raise the air temperature 10° C on a clear summer day. Therefore, if an air-conditioned greenhouse is built in which the air is changed twice a minute, as we have in Pasadena, the exhausted air is 5° warmer than the air entering the greenhouse. This explains why non-airconditioned greenhouses have to be shaded or whitewashed in summer. If full sunlight were permitted to enter, the temperature would rise so high that the plants would be injured or killed by the heat, or, as commonly said, they would be burned. In a properly air-conditioned greenhouse no shading is necessary, even on the hottest days, and many plants which are considered shade-loving can be grown in full light the year around (for instance orchids like *Phalaenopsis* and *Cattleya*). Therefore, by air-conditioning we can take full advantage of the sun's radiation in a greenhouse.

In Pasadena, at the California Institute of

Technology, a new laboratory has been built where these principles have been applied. In the Earhart Plant Research Laboratory there are 6 completely air-conditioned greenhouses, which can be kept at different temperatures and humidities, 13 artificial light rooms in which also temperature and humidity can be controlled, an equal number of dark rooms, and in addition the artificial light rooms can be separated by curtains into compartments with different photoperiods. Thus we can maintain simultaneously about 50 different conditions. In addition, there are a wind tunnel, fog and rain room and gas rooms. In all these rooms temperatures are kept constant.

Under such completely controlled conditions something new in botany appears: complete uniformity of experimental plants grown under such controlled conditions. In this way the genetic purity of our seed material becomes translated into such uniformity of phenotype that we can materially reduce the number of experimental plants, and that often we can dispense entirely with statistical treatment of the experimental results.

Since in nature the plants are subjected to fluctuating temperatures, the constant conditions are not natural, but by moving the plants from one condition to another, almost any combination of temperature and light can be produced. To this end the plants are placed on small trucks, which can be wheeled from one greenhouse to another or to dark and light rooms. Thus we can maintain in this building simultaneously several hundred different conditions or combinations of conditions. This is of special importance in the investigation of growth as a function of "climate," since climate is not just expressible as one variable, but may mean the changing of many variables simultaneously. We have no basis for assuming that if temperature has a certain effect at one light intensity, it will have a similar effect at a lower or higher light intensity. In fact, we know that the responses are different. Therefore, in a study of the climatic response of a particular plant we must investigate practically each com-

bination of the more important variables. This can only be approached by studying simultaneously the effects of these different combinations. Thus we get a multidimensional relationship, the results of which we also have to express in a form more complicated than the conventional 2-dimensional graphs. We can for instance plot the growth rate of tomato plants on the vertical axis, and day and night temperature on the two horizontal axes of a 3-dimensional grid. To bring in still another variable, e.g. photoperiod, we would need a 4-dimensional grid. However, we can simplify the picture, by not plotting the actual growth figures, but by plotting the position of the optimal growing conditions, which removes one dimension. We must realize in such a presentation that the optimal growing condition *only* is represented by such a point, but that at slightly lower or higher temperatures growth still is good. Therefore the point is actually a spherical or ellipsoidal area in the 3-dimensional grid, which is gradually tapering off in all directions.

As best examples of the plotting of such data let me use some plants with which all of you are familiar. For some years we have been investigating, with support of Sunset Magazine, the optimal growth conditions of a number of common garden plants.

The English Daisy, *Bellis perennis*, died when it was grown continuously in the warm greenhouse. When the temperature during day was kept at 26° C, the plants only survived at night temperatures below 10° C, whereas at a day temperature of 18°, it would support nights as high as 15°. But flowering was only abundant at 8° night temperature. At longer photoperiods the plants would support slightly higher temperature, but the best plants grew at 14° day, 8° night temperature, and a 10 hour photoperiod. This point can be placed in the same 3-dimensional grid in which we plotted the average climate of Pasadena. Then we see that the climatic ellipse of Pasadena transects the optimal climate for *Bellis* in February and March. In nature we actually find *Bellis* flowering predominantly in February and March in

Pasadena. In cooler climates, with cooler summers, the climatic ellipse may cut the *Bellis* optimal climate in summer, and there it flowers all summer long.

Saintpaulia, the African violet, is a typical tropical plant. When it is grown continuously at 10° C during night it dies, and it does best at 25° C during day and 22° C during night. Therefore it can never be grown outside in Pasadena because the Pasadena climatic ellipse never reaches the *Saintpaulia* optimal climate. The gardening public can be divided very sharply into two camps, those who can and those who cannot grow African violets in their houses. These two groups are equally sharply divided into those, who keep their windows open during night, so that the room temperature drops much below 20° C, and those who keep the windows closed in the rooms where they grow African violets. Thus, if you tell me which plants you grow in your house, I can tell you how you live.

In the case of *Zinnia* we find that as young plants they require slightly higher temperatures than when they are flowering. Furthermore *Zinnia* is a short-day plant which requires reduction in the length of day for flowering. But to grow good vigorous plants one has to start them in long days. The same thing is true of *Cosmos*, or *Callistephus*. When these are subjected from an early age on to short days, they will flower very rapidly while very small plants, and are no good as garden plants. Thus, in the garden, short day plants should always be started in the long summer days. When we plot now the climatic requirements of *Zinnia* we find that the climatic ellipse of Pasadena transects the *Zinnia* area completely during the summer; actually Pasadena is one of the places where *Zinnia* seed is produced commercially.

In the same way we can plot *Petunia*, *Matthiola* (stocks), *Papaver nudicaule*, *Ageratum* and others. When we compare their optimal climates with the climatic ellipse of Pasadena, we find that in every case the graphic presentation indicates correctly when these plants grow best in that climate. By drawing in other climatic ellipses we can immediately see whether

a particular plant will do well in a particular locality, and what the best growing period is. If the plant climate is some distance removed from the climate where one wishes to grow it, this usually is possible, but the plant requires more care, because it could not stand up in competition with plants adapted to the particular climate in that locality. Still further removed from its optimal conditions the plant may die altogether, even though it is not subjected to any extremes in temperature which would cause freezing or heat coagulation of proteins.

When a plant is grown under its optimal conditions, there are two interesting phenomena to be noted. In the first place can such a plant stand competition with other plants, even weeds, without help from man. And in the second place is such a plant little affected by pests and diseases. The reason for this may lie in the fact that under optimal growing conditions sugars and other food components are used up at the fastest rate, keeping their concentration relatively low in the whole plant, making them unpalatable for aphids or saprophytic fungi.

The reasons for death of the plant under unfavorable conditions seem to lie in the response of the plant as a whole, and not of the individual cells. It is conceivable, though not conclusively proved, that under unfavourable temperatures no translocation within the plant occurs, causing starvation especially of the young tissues.

Let us consider now for a moment what the response to temperature means for a plant in the course of Evolution. Let us first take an example from the work of Dr. HIESEY of the Carnegie Institution of Washington. He has been growing different *Poa* species in the Earhart Laboratory. *Poa ampla*, a strain collected from Spokane in the state of Washington, flowered equally well at 20, 23 and 30° day temperatures. But for flowering it needed nights under 14°, at 17° it did not flower at all, even though vegetative development was good. Therefore this plant never could propagate itself in a fairly warm climate. We now know

many such instances. In certain cases closely related varieties or ecotypes differ in their night temperature requirements for flowering. For instance, again taking one of Dr. HIESEY's plants, *Achillea borealis*. A strain from the coast of California, which is dormant during the dry summers, flowers only when the nights are cool. But a form from the hot inland valley flowers much better with warm nights. If these two forms were growing side by side, in competition with each other, the warm interior valley form would be the only form which could reproduce in the warmer nights, whereas the coast form would reproduce better in cooler nights.

Another example can be given in the case of tomatoes. Fruit set and seed production in tomatoes is dependent upon a very narrow range of night temperatures. When the nights are too cold or too warm no fruits are produced. There are rather slight differences in optimal temperatures for fruit set between varieties. These slight differences in optimum are immediately reflected in large differences in yield. In La Jolla, California, the Beefsteak tomato, for instance, produced 8 kg of fruits per plant, and the Earliana only 6 kg. Nearby, in Temecula, where the night temperatures are about 3° lower, Earliana produced 8 kg and Beefsteak 2 kg. If in direct competition these two varieties only differed in their seed production in proportion to their fruit production, Beefsteak would disappear in Temecula within 5 years, and Earliana would be completely replaced by Beefsteak in La Jolla in 20 years. In the case of smaller temperature differences the time would be longer, but it is obvious that in counting with geological periods of time, very slight differences in temperature response of plants will exert a controlling effect on their distribution and survival.

In terms of agricultural applications it is also obvious, that a detailed knowledge of the temperature response of commercial varieties is essential. In that way the best variety for each particular climate can be selected with far fewer expensive field trials. Besides, a field trial in a

warm year may indicate other varieties to be best than in an average or cool year.

This leads to another possible application of knowledge about the climatic response of crop plants. As is already known in tomatoes, and suspected in other plants, their response to temperature is amongst the most important factors determining yield. Therefore a genetical analysis of the factors contributing to the temperature response might make possible a more logical breeding program. If we know for example that the flowering date in peas depends upon the temperature somewhat like $a + b(t^2 + c)$, then we can expect a , b and c to depend on genes, and thus any desired response to temperature could be bred for by combining varieties possessing genes producing the proper values for a , b and c . Many of you who have seen the magnificent successes of plant breeders and the contributions of cytologists to the development of new varieties here in Sweden may doubt whether much more advance could be obtained, yet I am convinced that once physio-genetics has had a chance to show its possibilities it will rank as a worthy younger brother with cytogenetics.

Most of the previous discussion was concerned with the vegetative development of plants, and it was found that in many cases a particular rather narrow range of climatic conditions could be specified within which optimal development occurred. In agricultural and horticultural plants it is easy to control the time of year when the vegetative development occurs, by proper sowing and planting dates.

In wild plants no such guiding human hand is available, and it becomes exceedingly interesting to see, how the timing is accomplished in Nature. I want to give a few examples and for these I have chosen some of the plants I am most familiar with in the mountains and deserts of Western America. In the Sierra Nevada and the volcanic ranges further North to Canada, we find at the higher altitudes in the alpine meadows that magnificent flower display for which the Alps are also so famous. At 2000–3000 m the flowering is restricted to a rather

short period in connection with the short growing season. The actual growing season at timberline at 3000 m is about 2 months, July and August. Earlier and later the nights are too cold. The ripening of fruit requires usually $1-1\frac{1}{2}$ month, and therefore flowering has to occur at about the middle of July. That gives a little over 2 weeks from the starting of growth after winter till flowering. Length of day would be an inadequate guide for these plants to bring them into development and flower, because around the end of June the photoperiod changes but little, and besides the dormant plant would probably be unable to perceive the light stimulus. Here the breaking of dormancy is a matter of low temperature. In the case of *Veratrum* we are investigating its dormancy, and it *only* can be broken by 6 months of temperatures very close to freezing. Once their dormancy is broken, vegetative development is explosive, and the flowers, which were formed in the previous season appear within 4 weeks after removal from 0°C. Other similarly controlled plants are *Erythronium*, or Avalanche lily, appearing within 2 weeks after melting of snowfields, very much like *Soldanella* in the Alps.

At lower altitudes we find the typical spring flora of deciduous forests, which must develop and mature between the end of winter in March and the leafing out of shading trees around May first. HARTSEMA has shown that for the Lily-of-the-Valley, *Convallaria*, the beginning of growth occurs also only after a cold period of about freezing temperatures which may be considerably shorter than for *Veratrum*. In all these plants, and in deciduous trees too, beginning of development is synchronized with sharp seasonal temperature changes.

It is superfluous to mention here the enormous importance of photoperiod in the seasonal development, primarily flowering, of many plants.

Let us now consider the seasonal development of plants in the deserts. This is perhaps the most complex of all seasonal phenomena. At irregular intervals of several years, occasionally a year occurs in which the usually vegeta-

tionless bottom of Death Valley in California blossoms out into a magic carpet of billions of yellow *Geraea* and *Oenothera*, white *Monoptilon*, blue and lavender *Phacelia*, and red and blue *Gilia*, with a sprinkling of the lovely *Malvastrum rotundifolium*. This is of course connected with rains, but not in any simple way. For instance, neither the cloudburst of September 1938 nor the heavy rain of October 1945 caused any flowering the following spring, but rains in November 1939 and November 1946 caused an unforgettable flower display in March of the following year.

Experiments in the laboratory and observations in nature have shown, that these different effects from rains at different times of the year are due to the temperature response of germination in these plants. When the temperatures after a rain remain around 10° C., then only the winter or spring annuals, like *Baeria chrysostoma*, *Bromus rubens*, *Gilia* spp. and *Plantago* germinate. When the temperatures are higher, around 15°, many *Oenothera* species, *Geraea canescens* and *Abronia* will germinate, with relatively few of the smaller winter annuals. At still higher temperatures, above 20°, none of the previous species develop, but *Bouteloua*, *Pectis*, *Amaranthus* and *Euphorbia*, all summer annuals, and typical desert shrubs like *Larrea* and *Acacia*, germinate. At higher or lower temperatures nothing germinates any more. Therefore the aspect of the vegetation especially as far as annuals is concerned, is completely different after summer, autumn or winter rains. An autumn rain in a desert near sea level may cause germination of summer annuals, whereas the same rain at a high altitude results in the establishment of winter annuals. There are only relatively few plants, like *Datura* and *Palafoxia*, which germinate at all temperatures.

It is not only *when* the rain falls, but also *how* much, which determines germination. In general there is no germination after rains of 15 mm or less. But 25 mm causes fair, and 40 mm or more results in full germination. Complete germination of all viable seeds means populations of up to 5000 individual plants per square

meter. Such densities produce carpets of plants, which are already green a few days after the rain. The most amazing fact about this excessive plant density is, that usually well over 50 per cent of all these plants will flower and set fruit. Once germination has taken place, each seedling will continue its development and no selection occurs any more. Therefore it is the germination stage during which natural selection has to take place. This is probably the reason, why such a large variety of special germination mechanisms has developed in these desert plants. The survival of these annuals is not a matter of easy germination, but depends upon all sorts of germination controls, which will prevent the seeds from germinating when the rains were not sufficiently abundant or did not come at the right time to insure complete development of the plant.

From the previous examples it can be seen to what extent the occurrence of plants is controlled by environmental factors, which can conveniently be investigated in air-conditioned laboratories. Research in the field of Physiological Ecology can explain much of the distribution of plants over the earth. It should be developed much more in the coming years, to insure a better integration of Ecology and Physiology.

I do not know whether this talk has perhaps made the impression of an apology for the air-conditioned greenhouses we now have in Pasadena. If not, I may not have said *enough* for the use of rigidly controlled growing conditions.

There is absolutely no doubt that for the solution of many problems in the Plant Sciences we need plant material of greater uniformity and growing conditions under better control. This need not be any more a pious wish, it is perfectly feasible. If in the average country a research worker's salary and research allowance were capitalized, this sum would be sufficient to build an ample structure with several controlled rooms and greenhouses, and probably even pay for its maintenance. Such a building would be sufficient for several research workers. Because of the greater reproducibility of the

experiments the results would be more significant; the number of replications could be reduced, and thus the effectivity of each research worker is at least doubled. Therefore at the capitalized cost of one research worker several others become twice as effective. This means that it is no longer a question whether an Institute or University can *afford* a building with air-conditioned rooms and greenhouses; on the contrary, a progressive administration *cannot* afford *not* to have such a structure.

I also hope that such better experimental facilities will draw together Plant Scientists from all different fields, because in a building

like the Earhart Plant Research Laboratory not only Plant Physiologists, but also Morphologists, Experimental Taxonomists, Anatomists, Geneticists, Agriculturists, Horticulturists, Biochemists and others find now unexpected possibilities, and thus I hope that the new development in air conditioning greenhouses will form a new tie between botanists of all denominations and produce a new more unified science. I hope to receive many of you as visitors at the Earhart Laboratory, where a limited amount of space may be made available for special research.

RESOLUTIONS

Resolution 1

The Jakob Eriksson Prize Fund

The Botanical Section of the IUBS proposes that the Jakob Erikssons Prize Fund, established at the Phytopathological Congress in 1923 and, when Phytopathology was merged as a section into the Botanical Congresses, entrusted by the Amsterdam Prize Distributing Committee to Professor N. E. SVEDELIUS of Uppsala in 1935, shall be entrusted to the Royal Swedish Academy of Science which has promised to administer the fund, if requested to do so;

that, the fund being too small for distribution of prizes in cash, the return for five years shall be used to coin a Jakob Eriksson gold medal;

that the Botanical Section of the Union, through a committee of experts, elected by the section, shall nominate a candidate of distinction, belonging to the younger generation, for this award, in recognition of his research in mycology, in plant pathology or in virus diseases, or of a particular publication dealing with such subjects, with the understanding that the work being so recognized is of a distinct international value and merit;

that the name of the candidate is submitted to a forthcoming congress for making the award.

These proposals were originally made by the National Swedish Committee for Botany and unanimously passed by the Botanical Section of the Union on July 11, 1950. They are brought in before you with the recommendations of the Resolutions Committee.

C. SKOTTSBERG

Resolution 2

It is recommended that a Commission for Plant Raw Materials (Pflanzliche Rohstoffe; Matériaux végétales crudes) be established in the Botanical Section of the International Union of Biological Sciences as requested by the memorandum signed by 58 scientists from 22 countries and by the paper presented by Professor REGEL in the Section for Agronomic Botany and that this commission be permitted to operate under its own regulations and budget.

It is recommended by the section for Agronomic Botany that a section of Plant Raw Materials be organized at the next International Botanical Congress.

Accepted in the Section of Agronomic Botany

ERIK ÅKERBERG

Resolution 3

The decisions of the Section of Nomenclature as accepted by the Seventh International Botanical Congress are found in the report by the Rapporteur Général (pages 457-550).

The Standing Committees appointed by the Section of Nomenclature and confirmed by the Congress are as follows:

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² Deceased January 19, 1951.

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Resolution 4

7^e Congrès Internat. de Botanique
Section de Phytogéographie

Vœu

«La section de phytogéographie du Septième Congrès International émet le vœu que la résolution, votée en 1935 à Amsterdam, de rechercher une entente internationale pour la classification et la définition phytogéographique des climats soit confirmée. Elle charge le comité créé à reprendre les travaux en vue d'atteindre

le but visé. Les résultats seraient soumis pour discussion au prochain congrès international.

La commission serait rattachée, comme sous-commission à la Commission d'Ecologie et géographie botanique, créé à Cambridge, appartenant à la Section botanique de l'Union internationale des sciences biologiques.»

Présenté par L. EMBERGER

Adopté à l'unanimité en séance du 18.7. 1950.

G. EINAR DU RIETZ

Resolution 5

Recommendation

Because the fundamental concepts in phytosociology are still matters of dispute, and because the techniques of description of phytosociologic units are—as a consequence of the above-mentioned disagreement—still widely varying, the section PHG of the Seventh International Botanical Congress considers it premature to lay down at the present moment more definite rules as to the nomenclature of phytosociologic units than those terminologic principles which were agreed upon by the Sixth International Botanical Congress.

K. FAEGRI

Accepted by the Section PHG, July 19, 1950.

G. EINAR DU RIETZ

Resolution 6

Recommendation

The section PHG of the Seventh International Botanical Congress considers that phytosociologists should in the future include in the description of phytosociologic units of whatever order a representative list of the species forming the community, if possible with indications of quantitative relations based upon statistical investigations.

K. FAEGRI

Accepted by the Section PHG, July 19, 1950.

G. EINAR DU RIETZ

Resolution 7

La Section PHG a proposé la constitution d'une *Commission pour les Cartes à petite échelle* notamment la Carte du Monde à 1/1 000 000^e.

Cette commission serait chargée d'étudier les principes de rédaction de ces cartes représentant les types de végétation et les culture. Les conclusions de ses travaux seraient présentées au prochain congrès international de botanique.

La Section PHG émet le vœu que cette commission soit rattachée comme sous-commission à la *Commission d'Ecologie et Géographie botanique* créée à Cambridge, elle même déjà intégrée à la *Section botanique de l'Union des Sciences biologiques*.

Les membres proposés provisoirement seraient: MM. ALLAN, BHARUCHA, CAIN, DANSE-REAU, GAUSSEN, HUECK, HUMBERT, NEGRI, DU RIETZ, SCHMID, SUCATJEV, VAN STEENIS, TROCHAIN, TROLL.

M. GAUSSEN assurera la liaison entre les membres et avec l'Union géographique internationale jusqu'à la première réunion où le bureau sera élu.

La resolution a été adoptée par la Section PHG

G. EINAR DU RIETZ

Resolution 8

The algologists gathered together at the Seventh International Botanical Congress in Stockholm consider that, from the point of view of the needs of taxonomic and physiological research, it is absolutely necessary to preserve the pure cultures of species and varieties already in existence and, further, that it is desirable that these collections be greatly extended.

We beg to propose that the persons named below be accepted by the Congress as forming a committee to forward and elaborate these proposals:

Dr. P. BOURELLY (France).

Prof. C. B. VAN NIEL (U. S. A.).

Prof. E. G. PRINGSHEIM (England).

Prof. F. SKOOG (U. S. A.).

Prof. G. M. SMITH (U. S. A.).

Prof. W. VISCHER (Switzerland).

Accepted by the Section of Taxonomy: Cryptogams.

JOHN AXEL NANNFELDT

Resolution 9

It is strongly recommended that the existing institutions of taxonomic botany recognize the need of having properly balanced departments or sections for cryptogamic taxonomy and geography, each department or section to be comprised of specialists in the major groups.

Proposed by G. EINAR DU RIETZ

Seconded by HOLTUM and DONK

Accepted by the Section of Taxonomy: Cryptogams

JOHN AXEL NANNFELDT

Resolution 10

Formation of an International Association for Plant Taxonomy and a Bureau for Plant Nomenclature

It is resolved that there be established an International Association for Plant Taxonomy with a Bureau for Plant Nomenclature and Taxonomy, and that the Association and Bureau include the International Commission for Botanical Nomenclature, the Standing Committee for urgent taxonomic needs and the International Commission for Plant Taxonomy.

Il est résolu qu'une Association internationale de Phytotaxonomie sera formée, avec un Bureau pour Nomenclature et Taxonomie, et que l'Association et le Bureau comprendront la Commission Internationale pour la Nomenclature, le Comité Permanent pour les besoins urgents de taxonomie, et la Commission Internationale de Phytotaxonomie.

Es wurde beschlossen, eine Internationale Gesellschaft für Pflanzentaxonomie zu bilden mit einem Büro für Nomenklatur und Taxonomie, ferner, dass mit der Gesellschaft und dem Büro die Internationale Nomenklatur

Kommission, das permanente Komitee für dringende taxonomische Bedürfnisse und die Internationale Kommission für Pflanzentaxonomie einverleibt werden.

Accepted by the Sections Taxonomy: Cryptogams and Taxonomy: Phanerogams

ERIC HULTÉN JOHN AXEL NANNFELD

Resolution 11

It is recommended that future international botanical congresses include a section for the history of plants sciences, which section, concerning itself with such subjects as botanical history, bibliography and biography, will also offer an opportunity for papers and symposia dealing with the border-lands between the natural sciences and the humanities, such as ethnobotany, history of cultivated plants, ethymology and history of plant names, philosophy and methods of biology, methods of documentation, publication problems, etc.

Il est recommandé que les Congrès à venir comprendront une section historique, laquelle doit s'occuper des sujets comme l'histoire, la bibliographie et la biographie botanique etc., fournissant aussi l'occasion de présenter des études des régions limitrophes entre les sciences naturelles et les humanités, etc.

Accepted by the Committee of Resolutions after having been presented by Dr. VERDOORN.

C. SKOTTSBERG

Recommendation

Resolution 12

It is recommended that

1) in principle, the International Botanical Congresses be held alternately in Europe and outside of Europe.

2) that future international botanical congresses meet at intervals of from three to five years, the dates to be established after consulting the Bureau of the International Union of Biological Sciences in order to avoid as much as possible the selection of dates which would clash with those of other congresses.

Il est recommandé que

1) dans toutes les mesures du possible, les Congrès Internationaux de Botanique soient tenus alternativement en Europe et hors d'Europe;

2) les futures congrès internationaux de botanique soient tenus à des intervals de trois à cinq ans et que leur date soit fixée après consultation du Bureau de l'Union Internationale des Sciences Biologiques pour éviter autant que possible, la concurrence de dates avec d'autres congrès internationaux.

Es wird empfohlen, dass

1) wenn irgend möglich, die internationalen Botanikerkongresse abwechselnd in und ausserhalb Europa gehalten werden sollen;

2) die künftigen Kongresse alle drei bis fünf Jahre gehalten werden und dass die Zeit festgestellt wird nach Konsultation mit dem Büro der Internationalen Biologischen Union, um das Zusammenfallen mit anderen internationalen Kongressen wenn möglich zu vermeiden.

For the Resolutions Committee

C. SKOTTSBERG

Resolution 13

Three invitations were presented at the Opening Meeting—from France, the United States and Canada. The day before yesterday a fourth proposal arrived in a letter from Professor RIVERA of Rome, to have the next congress in Rome, but as this invitation, for which we are of course very grateful, did not have the same official character as the other three, and time did not permit us to communicate with Professor RIVERA, the Committee found that this invitation could not be taken up for discussion.

The following resolution was then passed:

It is resolved that the Eighth International Botanical Congress be held in Europe and that, in acceptance of the invitation of France, it be held in Paris, in 1954, the hundredth anniversary of the founding of the Botanical Society of France.

It is recommended that, in conformity with

Resolution 12, the Ninth International Botanical Congress be held in North America.

Il est décidé que le prochain congrès sera tenu en Europe, et, en conséquence, que l'invitation de la France est accepté, et que le Congrès sera tenu à Paris en 1954, à l'occasion du centième anniversaire de la Société Botanique de France.

Il est recommandé, en conformité avec la motion précédemment accepté (Resolution 12), que le congrès suivant aura lieu en l'Amérique du Nord.

Es wurde beschlossen, dass der 8. Kongress

in Europa stattfinden soll. Demzufolge wurde die Einladung Frankreichs angenommen, den Kongress anlässlich der Hundertjahrfeier der Französischen Botanischen Gesellschaft in Paris im Jahre 1954 abzuhalten.

Es wurde empfohlen, in Übereinstimmung mit dem schon gefassten Beschluss (Resolution 12), dass der 9. Kongress in Nordamerika stattfinden soll.

For the Resolutions Committee,

July 20, 1950.

C. SKOTTSBERG

VOTES OF THANKS

THE PRESIDENT:

Representatives from various countries have asked permission to say a few words on this occasion, a permission which it is a pleasure to grant them. In order to save time, many countries have decided to present their greetings through a common spokesman. Thus, the only procedure possible will be to call upon the speakers in alphabetical order.

Professor Dr. HIKMET BIRAND,
Universität Ankara, Ankara, Türkei:

Herr President, meine sehr verehrten Damen und Herren!

Im Namen der türkischen Delegierten und derer unseres Nachbarlandes Israel möchte ich Ihnen und dem Organisationskomitee des VII. Internationalen Botanischen Kongresses meinen herzlichsten Dank aussprechen.

Die wissenschaftlichen Leistungen unserer schwedischen Kollegen waren uns ja allen längst bekannt. Durch diesen Kongress haben wir aber auch Gelegenheit gehabt, Ihr schönes Land, Ihre Arbeitsstätten und nicht zuletzt auch Ihre Gastfreundschaft kennen und schätzen zu lernen.

Ich möchte hier auch nicht die Gelegenheit versäumen, alle die Vertreter der hier versammelten Nationen noch einmal zu begrüßen und wünsche sie alle auf dem nächsten Kongress in bester Gesundheit wieder zu treffen.

Lassen Sie mich zum Schluss dem Wunsche Ausdruck geben, einen der nächsten Internationalen Botanischen Kongresse in nicht allzu ferner Zukunft in unserem Lande, das jedem Botaniker viel Interessantes zu bieten hat, versammelt zu sehen.

Auf Wiedersehen!

Director GERALD AGESILAU A. BITANCOURT,
Instituto Biológico, São Paulo, Brasil:

Au nom des représentants des Pays de l'Amérique Latine au VII Congrès International de Botanique, je remercie vivement ses organisateurs pour l'accueil chaleureux qu'ils nous ont fait et je les félicite pour le grand succès du Congrès.

Nous retournons dans nos pays, remplis d'admiration pour l'excellence des institutions scientifiques de la Suède et la haute valeur de ses savants.

La beauté de la ville de Stockholm et de ses

monuments, le charme et la douceur de la campagne suédoise, resteront longtemps gravés dans notre mémoire.

Nous faisons des vœux pour que les savants suédois puissent continuer leur labeur fécond, sans les soucis et l'inquiétude qui malheureusement nous assaillent encore aujourd'hui, pour que les liens d'amitié qui se sont établis ou renoués pendant le Congrès, contribuent pour leur part, à cette meilleure compréhension entre les hommes de toutes les nations, qui devra conduire un jour à la paix du monde.

Director **ALBERT F. BLAKESLEE**,
Smith College, Northampton, Mass., U.S.A.:

It is a pleasure on behalf of my countrymen to express to you, Mr. President, and to your colleagues our appreciation for all you have done for our entertainment and enlightenment. You have truly spread before us a bountiful *smörgåsbord* of botanical information of which, alas, we have been able to taste only a few samples. I represent the United States of America where it is possible to travel 3 or 4 days by express train without changing currency or having our baggage inspected. A political United States of Europe has not yet been established. However, from my recent investigations here in Stockholm, I find that in one respect you really are a United States of Europe. You are pretty well united in your state of mind regarding the "Life Saver" confections which I provided for you. You do not like the flavor of wintergreen which to us Americans is very pleasant. My study is leading me to believe that it is familiarity with the odor which makes the difference.

We have met here botanists from Sweden and from countries outside of America, who were known to us only as esteemed names in the literature. We have now become familiar with them and find them personally very pleasant. We shall leave Stockholm with many new friends and with pleasant memories. To you and your coworkers of this successful congress we say with deep feeling but with faltering accents: Tack så mycket!

Professor **Dr. F. BUSTINZA**,
University of Madrid, Madrid, Spain:

Mr. President, Ladies and Gentlemen:

On behalf of all the Iberian botanists from Portugal and Spain, who have come to this beautiful Stockholm to attend the Seventh International Botanical Congress, I wish to express to all our deepest gratitude for the kindness and the generous and cordial hospitality which we have received during these days.

I should also like to congratulate the President, Professor **SKORTSBERG**, the Secretary General, **Dr. ÅBERG**, and all the members of the Executive Committee for the perfect organization, and for the complete success of this Congress, which not only has enabled us to become aware of the program realised in recent years in the botanical field, but has also enabled us to get into contact and strengthen the relationship between all the members of the great international family of scientists, whose aims are only peaceful, because our objective is the progress of the botanical science and consequently the progress of civilization, always at the service of mankind.

But I should also like you to allow me to say a few more words, since we, the Portuguese and the Spaniards, owe a great debt of gratitude to Swedish botanists. It would be unpardonable if, being in the country of **LINNAEUS** and **LÖFLING**, we did not take advantage of this moment to express our profound admiration for your famous botanist **Löfling**, the first and most beloved disciple of your genius **Linnaeus**. We recall that **Löfling** was sent to Spain by **Linnaeus** in 1751. He worked at the Botanical Garden in Madrid. He collected plants in the plains and mountains of Portugal and Spain and carried out brilliant work in connection with the study of the Flora of the Iberic Peninsula. And I should also like to recall that **Löfling** died in 1756 on a scientific mission patronised by Spain in the **Mercuri** expedition to a zone of South America that now belongs to Venezuela.

In recalling to you today the glorious name

of Löffling, I should like to state that the Iberian botanists will always remember him with the deepest gratitude, since he came to our country to work and enthusiastically devoted the last years of his life to the study of the Flora Hispanica. Tack så mycket!

Professor THEM. DIANNELIDIS,
Institute de Botanique, Thessaloniki, Grèce:

Monsieur le Président!

En ma qualité de représentant de la Grèce, pays des éminents fondateurs de la botanique Aristote et Théophraste, je suis particulièrement heureux de vous exprimer, ainsi qu'aux membres du comité, mes sentiments de profonde gratitude pour l'accueil si bienveillant qui nous a été réservé dans votre noble pays, lié à la Grèce par des liens de traditionnelle amitié.

Professor Dr. J. FITTING,
Bonn a/Rhein, Deutschland:

Hochgeehrter Herr Präsident Skottsberg!
Sehr verehrte schwedische Herren Kollegen!

Als uns an dieser Stelle vor wenigen Tagen aus bereitem Munde ein historischer Überblick über die früheren internationalen botanischen Tagungen gegeben wurde, ist es wohl jedermann klar bewusst geworden, wie sehr dieser Stockholmer Kongress alle andere in den Schatten gestellt hat. Eine bisher noch niemals dagewesene Hochflut von Teilnehmern drohte, alle Dämme zu sprengen. Infolgedessen war auch die Fülle an grösseren und kleineren Vorträgen aus allen Gebieten der Botanik ganz überwältigend und für den Einzelnen kaum mehr überblickbar.

Wir Aussenstehenden, ich möchte fast sagen, wir Geniesser dieses Kongresses, vermögen wohl kaum ganz richtig einzuschätzen, welche Fülle zeitraubender und aufopfernder Arbeit mit seiner sorgfältigen Vorbereitung verbunden war. Ich meine aber, alle die Persönlichkeiten, die sich um das gute, reibungslose Gelingen

unserer diesjährigen internationalen Botanikerzusammenkunft hohe Verdienste erworben haben, dürfen die beglückende Gewissheit von ihr mitnehmen, dass auf ihrer hingebenden Arbeit reicher Segen geruht hat.

Von den Herren Kollegen, deren *Muttersprache deutsch ist*, wurde mir der ehrenvolle Auftrag gegeben allen Damen und Herren, denen die Vorbereitung und Durchführung unserer Tagung obgelegen hat, wärmsten Dank für ihre Mühewaltung auszusprechen.

Vor allem geziemt es uns, Seiner Königl. Hoheit dem Kronprinzen Schwedens unseren ehrerbietigsten Dank dafür abzustatten, dass er uns Botanikern die hohe Ehre erwiesen hat, den Kongress mit einer eindrucksvollen Ansprache zu eröffnen und uns danach im Drottningholmer Schloss huldvoll gastlich zu empfangen.

Nächst dem gebührt unser wärmster Dank in erster Linie Ihnen, hochgeehrter Herr Präsident SKOTTSBERG. Als princeps botanicorum, gewissermassen ein botanischer Nachfahre des grossen LINNÉ, haben Sie unseren Kongress meisterlich mit souveräner und doch auch sanfter Hand geleitet. Nicht weniger gilt unser Dank den schwedischen Vizepräsidenten unserer Tagung, dem Generalsekretär, Herrn Dr. EWERT ÅBERG, auf dessen Schultern monatelang gewiss eine ganz besonders schwere Arbeitslast gelegen hat, allen Mitglieder der verschiedenen vorbereitenden Organisationskomitees, den Herren Präsidenten der zahlreichen Sektionen, sowie überhaupt allen Damen und Herren, die vor und hinter den Kulissen sich für ein gutes Gelingen dieses grossen botanischen Welttheaters tatkräftig eingesetzt und sich während seines ganzen Verlaufs so überaus hilfsbereit um uns bemüht haben. In besonderer Dankbarkeit möchte ich hier ferner aller schwedischen Kollegen gedenken, die uns als Leiter zahlreicher hochinteressanter botanischer Exkursionen vor, während und nach dieser Stockholmer Tagung in die Eigenheiten der naturwissenschaftlich so fesselnden Natur des Schwedenlandes und in seinen Pflanzenbestand eingeführt haben oder noch einführen werden

und uns einen Einblick in seine beneidenswert ausgestatteten, schönen botanischen Institute haben tun lassen.

Und nicht zuletzt ist es uns ein Bedürfnis, allen massgebenden Stellen in den Städten Stockholm und Uppsala herzlich dafür zu danken, dass sie uns durch genussreiche, gesellige Veranstaltungen verschiedener Art eine sehr willkommene Entspannung von der Kongress-tage Arbeitslast in Stockholm und Uppsala verschafft und unseren wissenschaftlich nicht tätigen Damen den Aufenthalt in Schweden so unterhaltend und belehrend gestaltet haben.

Vielen von uns hat sich erst durch diesen Kongress ein alter Wunsch erfüllen lassen, unsere schwedischen Kollegen, deren botanische Forschungen seit LINNÉ's Zeiten in unserer Wissenschaft stets einen hervorragenden Rang eingenommen haben, deren Namen und botanische Arbeiten uns daher nicht unbekannt geblieben waren, einmal persönlich in ihrer schönen Heimat kennen zu lernen. Das aber halten wir für einen ganz unschätzbaren Gewinn.

Dieser Kongress bildet daher in unserem Leben in vieler Hinsicht einen Höhepunkt. Wir werden zeitlebens an ihn und seine schwedischen Veranstalter in herzlicher Dankbarkeit freudig gedenken.

Professor Dr. F. E. FRITSCH,
Cambridge, Great Britain:

I feel that I am all unworthy to speak for my many colleagues that have come to attend this Congress from among the British Commonwealth of Nations, the more as they number many men and women occupying a more distinguished position than I in the field of botanical science. In fact the chief qualification that I can find, apart from age, is that I represent the Linnean Society of London that has the conspicuous honour of including among its Honorary Members, His Majesty the King of Sweden and that has so long maintained a friendly connection with this country, the fatherland of CARL V. LINNÉ. For many of

those for whom I am now speaking the visit to the home and garden of LINNÆUS in Uppsala and to his country home has no doubt been one of the highlights of the Congress, but we shall also treasure memories of the address with which his Royal Highness, the Crown Prince, inaugurated the Congress and the gracious reception we received from him when we visited Drottningholm on the same afternoon.

We have all derived inestimable benefits from the contacts we have made with your many brilliant botanists. For some of us these were a renewal of old friendships, but many will have met most of their Swedish colleagues for the first time. We have admired your scientific institutions and have fully enjoyed the beauty of your city of Stockholm. We have been charmed by the courtesy and kindness we have received and are full of gratitude for the manifold hospitality you have afforded us. On behalf of all those who have attended this Congress from the British Commonwealth of Nations I tender you, sir, our heartfelt gratitude and express the hope that you will convey our thanks to all those who have contributed to the undoubted success of the Congress and have ministered to our comfort and pleasure.

M. le Professeur ROGER HEIM,
Paris, France:

Monsieur le Président!

Les botanistes de langue française, ceux de la Belgique, de la Suisse romande, les botanistes canadiens français, ceux de l'Union Française et de la France, m'ont confié la mission, dont je mesure tout le prix, de vous apporter l'expression de notre gratitude. Pour mieux illuminer votre accueil vous avez su déchirer le voile de nuages qui glissait au-dessus de votre ville, si fièrement campée dans le jet de ses édifices, et nous livrer un ciel parfois si bleu que nous avons voulu y découvrir comme le destin de votre pays.

Au nom des botanistes de langue française, j'exprime aussi notre pensée reconnaissante

au secrétaire général de ce Congrès et à tous ceux de vos compatriotes qui se sont voués à la tâche difficile de faire face à cet immense peuplement cosmopolite, à la fois botanique et humain, dont l'introduction artificielle, et passagère, n'aura, je l'espère, provoqué aucune rupture dans les équilibres naturels de vos biocénoses.

Lointaine et incomparable tradition de vos naturalistes, persévérance et rigueur de vos expérimentateurs, richesse de vos archives vivantes, organisation modèle et moderne de vos Instituts, la Suède s'est révélée à ceux d'entre nous qui l'ignoraient encore, comme un grand pays, car ce n'est point à l'espace qu'on juge de l'œuvre mais à la profondeur des fondations. Et les vôtres sont rudement rocheuses.

Nous avons vécu votre histoire depuis Linné jusqu'à Nobel, depuis les tumuli du vieil Uppsala jusqu'au joyau puissant que vous a légué Ragnar Östberg, et qui domine votre ville, face aux horizons, comme un symbole non seulement de votre génie national, mais de votre vigilance.

Nous vous quitterons bientôt, demain déjà, enrichis de votre exemple, éclairés par votre hospitalité. Mais l'écho de notre amitié répètera souvent cette phrase que je lisais ce matin, écrite au dessus du tombeau de vos rois, dans votre Eglise de Riddarholm: *De loin comme de près.*

J'ai donc le très grand honneur de représenter ici ceux qui depuis Bruxelles jusqu'à Genève, et de Fribourg à Montréal, et partout par le monde, à Léopoldville et au Parc Albert, à Saigon et à Dakar, sont attachés à une forme de pensée, à une certaine structure de l'esprit, à un certain mode de logique, qui se prolonge dans une langue qui nous unit, Canadiens Français, Suisses romands, Belges de Wallonie et Français. Mais cette langue qui fut celle de Voltaire et de Maeterlinck, de Ramuz et de Ringuelet, celle de Lamarck et des De Candolle, elle n'est point l'instrument de nos réflexions, elle est la musique de notre esprit, et sans doute, elle aussi, indispensable au monde. C'est pourquoi nous avons enregistré, non point par un nationalisme étroit, mais bien par la seule conscience de notre rôle, le progrès que le fran-

çais a pu, cette fois déjà, réaliser au cours de nos débats, grâce notamment à tous ceux de nos amis étrangers qui se sont exprimés parfaitement dans notre langue.

L'équilibre harmonique dans l'importance que les langages ont acquise, de même que l'équilibre raisonnable et raisonné des espaces auxquels les peuples ont droit, est un garant du maintien de la civilisation mondiale.

Cet équilibre linguistique, hélas!, ne suffit point.

Aujourd'hui, devant nous, un nouveau pont s'amorce. Nous avons laissé une arche derrière nous. Nous sommes au milieu d'un fleuve qui bouillonne. Devant nous, comme en 1935 à Amsterdam, la route disparaît vite dans le brouillard. Durant ces quatre années qui viennent au bout desquelles nous avons pris rendez-vous, elle sera longue parce qu'elle sera dure. Souhaitons qu'elle le soit plus pour les gouvernements que pour les peuples.

Pourtant, une fois encore, nous avons prouvé, ici, aux autres hommes, que la sympathie qui se contracte entre ceux qui vivent de la même passion, de la même raison, dans la même activité, pour un même idéal, d'Objectivité et de Vérité, par la valeur du fait, que cet intérêt conduit à l'amitié dans l'union.

Botanistes de tous pays, vous avez créé en quelques jours à Stockholm la vraie société des peuples. Puissent tous nos gouvernements s'inspirer de notre réussite.

Dans ce monde qui, comme une fusée, va très vite vers un destin qu'il ignore, mais d'où il pourrait retomber en poussière, comme un immense feu de Bengale, dans ce monde où la technique et la machine livrent à l'homme, qui les a créées, le combat le plus perfide pour l'esprit — c'est notre façon de penser à nous autres qui parlons français —, dans cette Nature que l'homme, chaque jour, meurtrit un peu plus, semant autour de lui l'érosion par ignorance et cupidité, et le désert par l'érosion, dans ce monde dont la genèse doit à la plante tout son destin, nous sommes ceux qui vivons par elle et pour elle, nous demeurerons ceux qui veillons pour elle, pour l'avenir des autres.

La plante, elle n'est pas seulement l'objet de notre amour, la loi de notre curiosité, le plus bel éclat dans notre vision, elle est l'ouvrier de ce monde, celle qui sans cesse pousse et repousse, et ne périt que pour revivre, créant par ses dénouilles le lit de nos forêts, et par sa vie le creuset de notre propre vie. La plante, elle, est le salut des hommes.

Messieurs,

Vous nous avez fait à l'instant l'insigne honneur de choisir Paris pour lieu de notre prochain Congrès. Les Français vous en expriment leur fierté.

Au milieu des champs de tragédie où le blé a repoussé, cachant les traces des blessures sous la moisson,

Au milieu du champ de tragédie où le chèvrefeuille et le lierre auront alors recouvert, nous l'espérons quand même, les ruines et leurs deuils.

Paris, toujours debout, encore intact — par miracle,

Paris, et la France, vous attendent.

Professor Dr. GIOVANNI NEGRI,
Università di Firenze, Firenze, Italia:

Monsieur le Président — veuillez agréer les remerciements sincères avec lesquels la Délégation Italienne au VII Congrès International de Botanique prend congé de vous et de vos collaborateurs et vous prie de bien vouloir transmettre l'expression de sa reconnaissance à S. M. le Roi, qui nous a reçus dans son château à Drottningholm, à S. A. le Prince Royal, qui a bien voulu inaugurer nos travaux, aux autorités du gouvernement suédois et de la ville de Stockholm et des autres villes que nous avons visitées, qui nous ont fait bénéficier de leur hospitalité admirable et cordiale. Pendant cette brève période d'intense activité scientifique, de communications, de discussions, d'excursions, de visites aux Instituts admirablement outillés de vos Universités, de contact avec tant de maîtres, de collègues et de jeunes gens, dont plusieurs seront les maîtres de demain, nous emportons

chez nous, non seulement la satisfaction d'une si profitable expérience, mais aussi, et c'est, à mon avis, aussi précieux, des amitiés nouvelles, un souvenir ému, une sympathie intense pour votre pays si beau, pour votre peuple, si libre, si actif dans son calme, si simple dans sa prospérité, si avancé dans toutes les manifestations les plus nobles de la vie intellectuelle et civile. Vive la Suède et ses savants, Monsieur le Président, et merci encore.

Professor Dr. HARALD LINDBERG,
Helsingfors, Finland:

Högtärade presidium.

Mina damer och herrar.

På de danska, norska, isländska och finländska botanisternas vägnar ber jag att få säga några ord.

Det var med en känsla av glädje vi mottogo inbjudan till denna kongress. Vi kommo med stora förväntningar, vissa om kongressens glänsande förlopp. Dessa våra förväntningar ha icke gäckats, tvärtom medföra vi härifrån ett minne för livet. — Stockholm är känt som kongressernas stad, stadens sköna läge, rikssvenskarnas kända förmåga att ordna allt till det bästa för de väldiga skaror utlänningar, som vilja se och lära känna det väna landet Sverige, har gjort, att vi känt oss innerligt väl. Inget har stört trevnaden, t. o. m. vädret har varit gunstigt.

Under kongressens talrika förhandlingsdagar ha botanister från jordens alla hörn framlagt resultaten av sina ofta under många år bedrivna forskningar. Hundratals föredrag ha hållits över ämnen från botanikens alla områden; var och en deltagare har bland dessa funnit sådant som särskilt intresserat honom eller henne. Den största betydelsen har kongressen kanske dock haft genom att den möjliggjort den personliga samvaron deltagarna emellan. Gamla vänner och bekanta ha med glädje tryckt varandras händer. Nya bekantskaper ha gjorts.

Utfärderna till stadens omgivningar ha varit

trevliga och givande och skola länge kvarstå som ett angenämt minne.

Vi botanister från Nordens övriga länder vilja nu bringa dem, som burit dagens tunga, vårt innerliga, hjärtliga och broderliga tack och vilja vi samtidigt uttala vår varma önskan, att studiet av växtvärldens under här ständigt skall omhuldas med samma kärlek och framgång, och att botanisterna i LINNÉs land allt framgent skola stå i främsta ledet. — Vi önska även landet, som fostrat Eder, den bästa möjliga framtid.

Professor Dr. A. A. PULLE,
Utrecht, Netherlands:

Herr President!

I de holländares namn, vilka ha besökt den Sjunde Internationella Botaniska Kongressen, vill jag till Eder och Edra landsmän med några ord framföra mitt tack för den gästfrihet, som vi fått erfarra i Sverige.

I förhållande till invånareantalet i mitt land har det nederländska deltagandet varit mycket stort. Det bevisar icke endast att botaniken är en blomstrande vetenskap hos oss, utan också att holländarna ha glatt sig särskilt åt ett besök i ett land, vilkas invånare äro nära besläktade med dem. Vi ha icke heller glömt, att LINNÉ tillbringade tre av sina fruktbaraste levnadsår i Holland.

Vi äro tacksamma för allt vad Ni visat oss. Vi visste redan av de många berömda svenska publikationerna, att botaniken också blomstrar i Sverige. Vi har beundrat Edra moderna laboratorier, Edra vackra botaniska trädgårdar; vi har njutit av Edra mäktiga skogar och vackra sjöar.

Vår resa till Uppsala var en pilgrimsfärd till Eder store landsman CAROLIN LINNÆI verkstad. Vi är djupt imponerade av de många kultur- och konstföremål, som vi sett, inte minst av er arkitektur.

Många vänskapsband ha knutits mellan de holländska och svenska botanisterna.

Det må också vara mig tillåtet att tillfoga ett personligt tack för den stora gästfrihet, med

vilken jag har mottagits i Stockholm i ett hem tillhörigt en av Edra mest kända och ärevördiga botanister och hans maka.

Monsieur le Président!

Nous nous sommes trouvés chez vous dans un pays libre, parmi un peuple libre, qui connaît fort bien l'art de vivre, et l'art de bien-vivre.

Akademiker Dr. V. N. SUCATJEV,
Academy of Sciences, Moscow, U.S.S.R.

The Soviet Delegation wishes to thank the President, Secretary General and the Organizing Committee of the VII International Botanical Congress for the good organization of the Congress. The Soviet Delegation also thanks the municipal authorities of Stockholm for their hospitality.

We note with satisfaction that on the opening day at the Plenary session of the Congress we heard a report on the tasks of the botanists in resolving industrial and food problems, that the Congress had Agronomic Botany, Forest Botany and Phytopathology Sections and that a number of reports delivered at other sections were devoted to theoretical studies assisting in the solution of practical tasks. JOSEF VIS-SARIONOVICH STALIN, head of our state, a great scientist and thinker, repeatedly stressed that only such a science is true and advanced that does not separate itself from the people and that is ready to serve it willingly and voluntarily without being forced to do so. He said: "What sort of science would a science be that severed its ties with practice, with experience!"

Therefore in our country where huge tasks in the building of a new communist society are placed before science, botany plays an outstanding role as a theoretical basis for plant-breeding, cattle-breeding, forestry, for a number of industries, etc.

Difficulties and disagreements that come up in the path of development of our science are being resolved by a method of criticism and self-criticism, by means of free discussions. As an

example may serve the recent discussions on linguistics and problems of PAVLOV's theory in physiology in which our public took great interest. In a similar discussion victory was achieved by the MICHURIN theory in biology since this theory is a working theory, a theory of assistance to practice. This theory has been called the MICHURIN theory because MICHURIN discovered laws for the development of plant organisms and gave our country hundreds of very valuable varieties of plants.

The world of vegetation is fraught with boundless possibilities for meeting the needs of mankind. Rational use of these possibilities may yield a manifold increase in food resources, clothing and other material goods. Botany must assist in resolving this noble human task. Botany of this kind shall serve the cause of peace and its noble and great aim, that of promoting a universal peace.

The Academy of Sciences of the USSR—the center of Soviet science—has sent us to this Congress as representatives of the botanical science of all Soviet Republics—of the Russian Federation and the Ukraine, Latvia and Byelorussia, Estonia and Georgia, Lithuania and Armenia and of the other Republics that freely and voluntarily in a spirit of brotherhood united in the great Soviet Union. In connection with this the Soviet delegation deems it necessary to make a factual amendment to the opening speech of the President and to point out that the Baltic Republics which he said “are no more” have voluntarily joined the Union of Soviet Socialist Republics as three Republics enjoying full and equal rights, they have their own national Academy of Sciences widely assisted by the Academy of Sciences of the USSR.

As a token of gratitude to the Swedish people for its hospitality I should like to ask you, Mr. President, to accept our small gift—a set of volumes “Flora of the USSR” that have been published and to pass it on to some botanical institution in Sweden.

At the same time the Soviet Delegation intends to place on Monday a wreath on the grave of the great botanist LINNÉ.

THE PRESIDENT:

Messieurs,

Au nom du Comité organisateur je vous remercie de vos aimables paroles, trop aimables sans doute, mais témoignant de votre appréciation de nos efforts.

The President,

Professor C. SKOTTSBERG:

Ladies and Gentlemen:

Our congress is coming to its close, and I can only hope that you will look back on these days without feelings of discontent. I am quite aware of the fact that the organization has not been perfect and that misunderstandings and misadventures have occurred, but I hope that the pleasant memories will outweigh the less pleasant and that you will find that the scientific outcome of our meetings has given you what you expected or, if possible, even more. I have often heard people say that the only benefit of a congress is that it offers an opportunity to meet their colleagues, particularly those whose names and writings are familiar to them but whose personal acquaintance they would have no opportunity to make unless they could look them up in India or Japan, Australia or Hawaii, and so forth. Without underrating the significance of personal contact I wish to underline the importance of the scientific reports which enable us to keep in contact with what is going on right now. Last but not least, as manifestations of cooperation and goodwill our congresses are of inestimable value.

And now the time has come for me to thank all who have contributed to the success of this congress, if a success it be, and no duty could be fulfilled more willingly. From far and near you have flocked to this city, eager to give and take. No organization, however perfect, will warrant the success of a meeting like ours, only the high standard of the scientific contributions can do so, and I do believe that, from this viewpoint, our congress ranks second to none.

Vielen von Ihnen, und dies betrifft vielleicht besonders unsere deutschen und österreichischen Kollegen, ist es nur mit Schwierigkeit und durch persönliche Aufopferungen gelungen, nach Stockholm zu kommen. Wir brauchen nicht zu verhehlen, dass das Zusammentreffen mit Botanikern aus aller Welt nach diesen verhängnisvollen Jahren für Sie sehr bedeutungsvoll gewesen ist.

I feel greatly indebted to the Executive Committee for the support I have received from its members. Our indefatigable Secretaries-General, Dr. ÅBERG and Dr. NYGREN, have disregarded their personal interests for a long time and devoted themselves entirely to the interests of the Congress. I thank them for their zeal and energy and for having listened with great patience to my whimsical ideas without necessarily paying too much attention to them. Nobody has had a more thankless job than our Treasurer, Professor MALMSTRÖM; the warmer our thanks because he has put his skill at our disposal with a loyalty to our common cause

and a willingness of self-sacrifice which cannot be too highly praised. All of you have flown in and out of the buzzing beehive known as the Congress Bureau where you have met an army of young ladies who had undertaken to answer even the most impossible questions with courtesy and to assist you in every way, guided by Mrs. PRAVITZ and her seconds in command, Mrs. JACOBSSON and Mrs. AMINOFF. Their staff is so large that I cannot thank everybody in particular, but I hope that all of them will know how grateful we all are and how much we admire them for having stood this severe test so bravely.

Thanks are also due to the chairmen of sections and committees, to the recorders who carried the not too light burden of handling the programme, as well as to the excursion leaders and their helpers.

Finally, may I offer all of you members and participants of the Congress my humble thanks for the kindness you have shown me and for your indulgence with my shortcomings.

GENERAL EVENING LECTURES

LECTURE I

Friday, July 14th, 8 p. m.

Professor C. SKOTTSBERG, in the chair

Professor Dr. T. H. GOODSPEED,
University of California, Berkeley, Calif., U.S.A.:

*Illustrations of the Vegetation of Portions of Western South America*¹

The richness and variety of the floras of Colombia, Ecuador, Peru, Bolivia and Chile have attracted the attention of botanists from the start of the 18th century. Beginning with LOUIS FEUILLÉE who in 1709-1710 made plant collections near seaports in Chile and Peru, the botany of western South America has been made known by such men as JOSEPH DE JUSSEU (1735-1771, La Condamine Expedition, Ecuador, Bolivia, Peru), MOLINA, RUIZ and PAVON, MUTIS, NÉE, HUMBOLDT and BONPLAND, CALDAS, BERTERO, MIERS, POEPPIG, CUMING, GAY, DARWIN, SPRUCE, WEDDELL, PHILIPPI, TRIANA, RAIMONDI, REICHE, HERZOG, FRIES, WEBERBAUER, MACBRIDE, KILLIP, MUÑOZ, CUATRECASAS, ASPLUND, DUSÉN, SANTESON and the distinguished president of this Congress, Dr. CARL SKOTTSBERG, who has contributed so largely to our knowledge of the character and distribution of the floras of central and southern Chile, the Magellanic provinces and the Juan Fernandez Islands.

The labors of these and many other botanists and explorers, some of them actively at work today in western South America, have, however, produced only a partially complete picture of the distribution of the elements of a series of floras which exceed in diversity the extreme

variations in environmental factors existing over the thousands of kilometers separating Panama from Cape Horn.

The present-day greatly increased accessibility of remote areas, growing governmental interest in the exploitation of natural plant resources, reduction of health hazards in inhospitable environments by modern drugs but, particularly, the rapidly increasing effectiveness of local botanists, should see the virtual completion of the botanical picture of most of western South America in the next fifty years. One of the first steps in the realization of this objective will be the preparation of additional modern floras of West Coast republics. In this regard a high standard has recently been set by the botanists of the rest of South America by their Argentine colleagues. The *Genera et Species Plantarum Argentinae* is a convincing demonstration of the botanical advances made in Argentina during the past twenty-five years and of the national pride and of the prosperity of that great nation.

Western South America can be variously delimited in terms of its extent eastward from the coast of the Pacific ocean. For our purposes it extends in Colombia from the coast line to the high, cold *altiplano*; in Peru it extends eastward to the beginnings of the Amazonian rainforest and in Chile from the coast to the Argentine frontier. Much of the richness and of the diversity, as influenced by climates, of the vegetation of western South America so delimited has been described in the volume entitled

¹ In abstract form.

"Plants and Plant Science in Latin America" edited by Dr. FRANS VERDOORN who, because of this accomplishment and many others equally important and valuable, has placed the botanists of the world very much in his debt.

The photographs in natural color referred to in what follows were taken by members of five University of California Botanical Garden expeditions to South America. The first expedition was sent from Berkeley in 1935 and the other four were in South America in 1938-1939, 1942-1943, 1946-1947 and 1948-1949—a total of over four years during which the author and his wife and a number of North and South American collaborators made collections at various times and for varying periods in Colombia, Peru, Bolivia, Chile, Argentine, Uruguay and Paraguay. The original objective of these expeditions was a search for new or little known species and varieties of the genus *Nicotiana* and related genera. Ultimately, more and more attention was given to general plant collecting in areas that had not previously been botanized intensively or which were of some special phytogeographic significance.

Following this introductory statement the author showed one hundred and twenty-five 35 mm lantern slides in natural color. The first series illustrated the character and disposition of the unit collections in the University of California Botanical Garden at Berkeley. Many of the species grown in these collections were obtained by botanical expeditions sent from Berkeley to Western China and Tibet under the direction of Dr. JOSEPH F. ROCK, to the South American republics referred to above and to South Africa on which expedition Mr. ROBERT J. RODIN acted as botanist. The collection of the genus *Rhododendron*, many species of which were introduced by Dr. ROCK, contains over two hundred species and varieties while the representatives of South American floras contain an almost complete assemblage of the species of *Nicotiana* and include new or little known species of many other genera, with emphasis on *Orchidaceae*. A number of such species were shown. The material introduced

from South Africa added important elements to the research collection of cacti and other succulent plants which is now one of the most important in the United States. Slides of species of *Aeonium*, *Aloe*, *Agave*, *Titanopsis* and of *Ceropegia radicans* and *Frithia pulchra* were shown.

The following general summary of topographical features of the South American continent was documented with maps and charts. The continent extends from 12° N. to 56° S. of the Equator. On its western margin the massive Andean uplift rises abruptly and at times almost from the Pacific coast line to produce more terrain above 3000 m than is to be found in an equivalent area elsewhere on the earth's surface. Centrally are the interconnecting lowlands of the Orinoco, Amazon and Paraguay-Parana drainage systems. To the east, flanking and at times extending into these lowlands, are the extensive plateau regions of the broad Guiana and Brazilian highlands while farther south the Argentine pampa flows largely uninterrupted to the sea. Finally, there is the Patagonian massif, low yet higher than the pampa on which it abuts. The slides which followed showed the routes taken by the five University of California Botanical Garden expeditions and it was seen that in Colombia more attention was paid to the Depts. Antioquia and Valle del Cauca with some collecting in the upper Magdalena valley and more in the maritime Chocó mountain range; that Peru was rather thoroughly explored except the Amazonian hinterland; that the vegetation of Chile was studied intensively to but not below the island of Chiloé; that many phytogeographically significant areas in Bolivia, Uruguay and especially in Argentine, with emphasis upon Patagonia, were examined.

The following illustrations were then given of the climatic extremes or floristic distinctions existing in Colombia: first, the contrast between the high, semi-arid valley of Bogotá and the relatively nearby Pacific slope of Colombia beyond the maritime and portions of the central Cordillera which condense the ocean's moisture-

laden winds to bathe that slope in almost continuous rainfall (on parts of the Pacific slope of Colombia precipitation often exceeds 5000 mm and at times 8000 mm); second, the subtropical to tropical vegetation of Depts. Antioquia and Valle del Cauca and in particular the *Orchidaceae* of those areas; third, the seasonal climatic contrasts in certain regions along the course of the Magdalena river, which has its source in the central Cordillera and flows 1200 km to the Caribbean, with periods of drought producing a generally subxerophilous vegetation. Finally, a series of slides pictured the highland flora on the Nevado del Huila (Cordillera Central) from 2800 m to somewhat over 4000 m, the highest region in Colombia. Above the Subandean zone is a treeless, rocky terrain amongst the sparse herbaceous vegetation of which *Senecio latiflorus* is conspicuous because of its especially heavy, white and shining tomentum. In the famous páramos or high plateaus of Colombia, intensively studied by Dr. JOSÉ CUATRECASAS, the average low temperature, soil acidity, intense insolation and strong winds create a xeromorphous vegetation even though soil and atmospheric moisture is high. Species of *Espeletia*, *E. Hartwegiana* and others, dominate the vegetation of these exposed slopes, mixed with such rough fascicular grasses as *Calamagrostis effusa* and *C. recta*. The *Dracaena*-like appearance of the larger species of *Espeletia* and the dense, golden tomentum on their leaves and inflorescences make certain members of that genus of *Compositae* exceptionally noteworthy. Their tolerance of unfavorable climatic conditions was shown by their presence close to or actually on the snowline.

The next group of slides gave some evidence concerning major topographical and vegetational subdivisions of Peru. The Andean subdivision is dominant with extreme altitudes and a maximum width of over 300 km. From its eastern slopes the *montaña* or tropical rainforest, a second subdivision, flows down to the Amazonian plain. To the west below the largely semi-arid Andean foothills is the relatively narrow coastal strip, the third subdivision, which

approaches the absolute desert. The late Dr. AUGUSTO WEBERBAUER and Dr. FRANCIS MACBRIDE have adequately cataloged the vegetation of these three major phytogeographical areas of Peru and of the numerous subdivisions of each of them which are products of local variations in topography and climate.

Shifting sands and virtual absence of rainfall practically eliminate vegetation on the desert coast although in certain areas some woody species manage to exist, *Prosopis chilensis*, *Cryptocarpus pyriformis*, species of *Capparis* and *Acacia* and such grasses as *Distichlis thalassica* and species of *Tillandsia* are seen. During the southern winter from June to November heavy fogs blanket the coastal desert and its hills and mountains. Often for weeks and even months the sun only rarely penetrates this fog bank from which moisture condenses in quantity on the sandy soil. The effects of such winter moisture were illustrated by slides showing the sudden appearance of species of *Zephyranthes* on the subcoastal desert and nearer the sea species of *Solanum* and *Loasa* covering the surfaces of the sand dunes. On higher ground where more moisture is caught and condensed the typical *loma* vegetation appears—grasses which afford pasturage, *Compositae* in some variety and Begonias, delicate Peperomias, mosses and ferns in moister areas.

When water is abundantly available the subtropical climate of the Peruvian coast becomes apparent in the character and growth of both native and exotic plants. This situation was illustrated by views in Lima gardens and in the Jardín Botánico of that city of which the author is Honorary Director and which he redesigned and reorganized in 1943. Established over 150 years ago this Botanical Garden contains many native trees and shrubs planted there by RAIMONDI, the famous Peruvian geographer and naturalist, as well as collections of native cacti and related plants, orchids and other elements of the vegetation of the Amazonian portion of Peru.

The environmental and floristic sequence from the Lima region at approximately sea

level to the passes over the Cordillera at 5000 m was shown as follows: from Lima eastward along the valley of the Rio Rimac the arid hills are almost completely destitute of vegetation but where water from the river is diverted onto the arid plain cotton, principally, is grown with good success; above 1200 m occasional light rains permit a scanty herbaceous vegetation but the cacti dominate—for example, species of *Neoraimondia*, *Cephalocereus* and other genera, with xerophytic ferns at their bases—and nearby in favored situations *Carica candicans*, *Schinus molle* and species of *Caesalpinia* occur; at from 3500 to over 4000 m in the Peruvian *altiplano* (in central and southern Peru called *puna*) with snowy mountains nearby the climate is generally too inhospitable for successful agriculture and the natural vegetation is limited to perennial herbs, strong growing grasses and a few stunted trees—species of *Plantago*, *Meropia*, *Azorella*, *Werneria*, *Senecio*, the *ichu* grasses and such cushion cacti as *Opuntia lagopus*—but where there is water and protection from winds *quinua* and some maize as well as the Andean potato varieties are cultivated by the Indians.

A number of slides showed the series of plant associations and climatic states on the rapid descent on the eastern flank of the Peruvian Cordillera: the famous *ceja de la montaña* or eyebrow of the tropical rainforest, that misty, humid region of tree ferns and *Ericaceae*, epiphytes of all sorts and deep, mossy forest floor; the beginnings of the *montaña* or Amazonian rainforest along the Rio Huallaga, an affluent of the Amazon, where in abandoned agricultural developments species of *Cecropia* and other elements of the forest vegetation soon return the land to its original plant cover; the true *montaña* with its great floristic diversity including such well known species as *Lonchocarpus nicou* and representatives of the genera *Ochroma* and *Erythroxylon*.

Typical landscapes and plants of the southern Andes of Peru were next depicted: on steep mountain sides the sharp zoning of the vegetation with certain species as altitudinal markers;

the occurrence of semi-arborescent *Nicotiana tomentosa* in river bottoms at 1800–2000 m; above on wooded slopes epiphytes of many sorts, including orchids; somewhat higher numerous species of *Begonia*; still higher another species of *Nicotiana*, *N. Raimondii*, with such characteristic species as a *Tropaeolum* related to *T. tricolor*, the tall growing *Calceolaria tomentosa* and *Embothrium grandiflorum*.

To preface his discussion and illustrations of the floras of Chile the author showed a vegetational map of that geographically anomalous republic which has a length of over 4000 km and an average width of only ca. 150 km. The Andes occur in their highest expression in Chile and are absolutely dominant geographically. The central Chilean Cordillera rises abruptly from foothills to the perpetual snows of the Andean crest which forms the Chilean-Argentine frontier. In a strip 200 km from north to south this portion of the Andes contains numerous peaks above 4500 m and a number above 6000 m culminating in Mt. Aconcagua, the highest mountain in the two Americas, approximately 7000 m. The presence of the Andes as deflectors of tropical winds and robbers of the moisture of westerly ones, the occurrence of the Humboldt current along most of the Chilean coast and local topographic variations produce in Chile a variety of climates and a remarkable phytogeography.

The phytogeographical map that was shown will be used in a forthcoming account of plant distribution in Chile prepared by the author and Ing. Agr. EDMUNDO PISANO, until recently on the staff of the Ministerio de Agricultura, Santiago. In this map the whole of Chile is divided into the three general climatic and vegetational zones recognized from before the time of Reiche: the northern arid zone (18°–31° S.); the central temperate zone (31°–39° S.) and the southern humid zone (39° S. to Magellan Strait). In addition an Andean zone (18°–36° S.) is recognized. The sum of these phytogeographical subdivisions represents a north to south transition from subtropical aridity to a wet subantarctic environment, from essentially lifeless desert

through a Mediterranean region to a temperate rainforest. As elements of the major phytogeographical subdivisions a total of forty-eight plant formations and lesser groupings will be described in the article above mentioned.

The central or mesophytic zone was seen to have the Mediterranean type of climate on the coast and considerable aridity elsewhere. A central valley lies between the Andes and the Coast cordillera. South of Rio Bio Bio (37° S.) precipitation increased rapidly until, in the latitude of Valdivia and below, the annual rainfall in some areas exceeds 4000 mm, rain or snow falling throughout the year. Beginning in this area is the dense and sometimes impenetrable temperate rainforest made up largely of species of *Nothofagus*. The extremity of Chile has a coastal archipelago representing the partial submergence of the southward extension of the Andes with deep fiords cut into the mainland.

From Valdivia southward a succession of the dominant *Nothofagus* species occurs with, in the north, mixed stands of *N. dombeyi*, *N. obliqua* and *N. procera* and, at increasing altitudes, *N. pumilio* and *N. antarctica* and in the south *N. betuloides* and *N. nitida*. In the *Nothofagus* forests at least nine species of seven coniferous genera are found, the best known being *Araucaria araucana* and perhaps more famous botanically, *Saxegothea conspicua* and *Fitzroya cupressoides*. Among other features of Chilean plant geography referred to were the remarkable "islands" of south Chilean vegetation in the arid north central zone which have recently been discussed by MUÑOZ and PISANO and by SKOTTSBERG.

Illustrations were given of some of the characteristic herbaceous vegetation of the dry Chilean coast and almost equally arid foothills of the central Cordillera—numerous species of

Alstroemeria, *Mutisia*, *Puya*, *Cruckshanksia*, *Placea* and *Argylia*—and of the following species of *Trichocereus* (now growing in the Botanical Garden in Berkeley): *spachianus*, *Schickendanzii*, *pasacana*, *lampochlorus*.

Also shown were typical landscapes in the "Switzerland of South America" which is an appropriate name for the South Chilean region of deep, glacial lakes, extinct volcanoes crowned with snow, rapid flowing rivers and of dense *Nothofagus* forest.

The final series of slides showed something of the terrain and vegetation of Masatierra, one of the three islands of the Juan Fernandez group which lie from 670 km to 800 km west of the coast of central Chile. SKOTTSBERG's well known studies of Masatierra and Masafuera, on both of which collections were made by members of the University of California South American expeditions, demonstrate the fact that the flora of Juan Fernandez is quite remarkable and creates problems for the student of South Pacific and Antarctic phytogeography. One of the most striking features of this flora is the presence of 70 % of endemic species and ten endemic genera among the some two hundred species of indigenous vascular plants. Certain of these endemics such as arboreous genera of *Compositae* and *Umbelliferae* have no known relatives. For sailing ships from Europe coming round Cape Horn two hundred or more years ago Masatierra was usually the first landfall. They watered there and their scurvy-ridden crews sought something vegetable which was safe to eat and discovered that the growing point of the endemic palm, *Juania australis*, provided a wholesome salad. This beautiful palm and many other endemic species are now becoming rare. *Santalum fernandezianum*, cut for its fragrant wood by the old voyagers, had a worse fate and is now extinct.

LECTURE 2

Friday, July 14th, 8 p. m.

Professor ROB. E. FRIES, in the chair

Dr. W. B. TURRILL,
Royal Botanic Gardens, Kew, Richmond,
Surrey, Great Britain:

Curtis's Botanical Magazine

Every botanist attending this International Botanical Congress must be familiar with the Botanical Magazine. In a great many monographs of flowering plants the best citations of illustrations are simply quoted as Bot. Mag. t. so-and-so while many taxonomic problems have been first solved or elucidated in the pages of its text. Essentially it consists of coloured plates of plants grown in gardens in the British Isles with descriptive and explanatory accounts nowadays covering an average of 3 to 4 pages.

The aims of its editors and publishers have been, and are, two-fold: to provide a permanent record of cultivated flowering plants and to help botanists and horticulturists by increasing their knowledge of such plants as subjects of both taxonomic and gardening interest.

The Botanical Magazine has had a long history. It is, indeed, the oldest of botanical and one of the oldest of scientific periodicals still being published. It was founded by WILLIAM CURTIS and the first part appeared on 1 February 1787 with three plates, representing *Iris persica*, *Rudbeckia purpurea*, and *Eranthis hiemalis*. *Rudbeckia purpurea* is now generally called *Echinacea purpurea*, but the first and third of the names have remained valid and in general use up to the Stockholm Congress of 1950! This year volume 167 is in course of publication and this month's part brings the total of coloured plates to 9809.

It seems desirable first to give some information regarding the originator of the Botanical Magazine and the circumstances of its foundation. WILLIAM CURTIS was born in 1746 at Alton in the southern English county of Hamp-

shire. His father was a master tanner and a member of the Society of Friends, often known as Quakers. It is said that the boy William was introduced to the study of botany by the ostler of an inn near to his father's house. This ostler, whose name is variously recorded as JAMES, THOMAS, or WILLIAM LEGG or LAGG, possessed some old herbals and had a first hand knowledge of the local natural history. However, young CURTIS was apprenticed to an apothecary in Pudding Lane in the City of London and shortly afterwards moved to Gracechurch Street to another apothecary whose business and practice he later inherited. He sold this in 1770, for his heart was in botany, not in medicine. In 1773 he was elected "Demonstrator of Plants and Praefectus Horti" of the Society of Apothecaries—a high-sounding title with very small pay. He resigned in 1777. Meantime, CURTIS had commenced publication of the *Flora Londinensis*, that fine work of elephant folio size with hand coloured plates and descriptions of plants found within ten miles of London, and some others not native to the London area. The first part appeared in May 1775 and 72 parts in all were published by CURTIS, the last in 1798. The *Flora Londinensis* was a magnificent work and good copies are now valuable, but it was a financial failure and at the end of ten years from its commencement CURTIS was almost ruined by his too ambitious project. It is most probable that the concept of the Botanical Magazine arose as a result of his need to recuperate from the losses sustained over the *Flora Londinensis*. The Botanical Magazine was successful so that CURTIS became free from money worries and when he died from heart failure, on 2 July, 1799, he left his wife and daughter comfortably well off.

After CURTIS's death the Magazine was continued in general management and editorship

by his friend Dr. JOHN SIMS who remained responsible for its publication till 1826. At this date SAMUEL CURTIS, a nephew and son-in-law of WILLIAM CURTIS, owned the Magazine and his name appears as editor from 1827 to 1845. A new period opened up at the earlier date for the now well-established periodical, mainly because WILLIAM JACKSON HOOKER, then Professor of Botany at the University of Glasgow, became closely associated with its preparation. In 1845 the firm of Reeve Brothers (afterwards Lovell Reeve and Co.) acquired the rights and property of the Botanical Magazine. WILLIAM HOOKER, by then Sir WILLIAM HOOKER and Director of the Royal Botanic Gardens, Kew, became editor. The link thus forged with Kew, intimate though not formally official, has remained ever since, that is for over a century. WILLIAM HOOKER died in 1865 and was followed, both as Director of Kew and as editor of the Botanical Magazine, by his son Dr. (afterwards Sir) JOSEPH DALTON HOOKER who only resigned the editorship in 1904. For 77 years the HOOKERS, father and son, controlled the Botanical Magazine and themselves wrote a large majority of the text articles. Later editors were Sir WILLIAM THISTLETON-DYER, Sir DAVID PRAIN, Dr. OTTO STAFF, and Mr. A. D. COTTON. In 1920, with the last part of volume 146, there appeared an announcement that in consequence of the increasing cost of production the publishers proposed to terminate the publication of the Botanical Magazine with that part. After a short delay the Royal Horticultural Society took over the honourable but financially burdensome task of ownership and continued publication of the periodical. For nearly 30 years the Royal Horticultural Society has sponsored the Botanical Magazine, which, for this period has been one of the many links between Kew and Vincent Square.

After this brief historical outline of what might be called the external affairs of the Magazine we turn to say more about its contents. First, we deal with the plates and the artists who prepared the originals and then with the textual accounts.

The main characteristic of the Botanical Magazine has always been the coloured plates accurately portraying living plants. Most of the editors have therefore been dependent on trained botanical artists. It is not possible in a short time to analyse the work of all the artists employed since 1787 and a selection must be made. The great majority of the plates in the first forty-two volumes, nearly 1700 in all, were by SYDENHAM EDWARDS. Many of his original drawings are at Kew and are remarkable on account of their finish and accuracy. The plants they depict are easily recognized, though there are no analytical dissections. Their execution is simple and unlaboured and, as a rule, the colours are clear. The earlier plates were engraved by EDWARDS himself but later SANSOM was the engraver. For many years the colouring of the engravings was done by WILLIAM GRAVES who continued this work when EDWARDS and SANSOM ceased their connections with the Magazine in 1815. A certain J. CURTIS and then SWANN succeeded EDWARDS as artists. In 1826 there appeared some plates by W. J. HOOKER and for a number of years this extraordinary man acted as artist, author, and editor for the Botanical Magazine, in addition to all his other duties. His drawings are noteworthy for their boldness of conception and emphasis yet ease of execution. The plates began to be accompanied by analyses and were still engraved. HOOKER now found and trained in Glasgow a young artist, WILLIAM HOOD FITCH, who soon became a first-class botanical draughtsman. Not only did FITCH perfect the free and easy style in which he was trained by HOOKER but he learned lithography and from 1845 to 1877 he was both artist and lithographer for the Magazine. The change from engraving to lithography added to the beauty of the plates by the softer representation on the stone compared with the harder outlines of engravings. Moreover, since FITCH did his own lithography he was able to make his originals outline sketches rather than completed pictures. The result was that on the stone the drawings became somewhat generalized but, thanks to FITCH'S

accurate visual memory they thus often better represented the species than would photographic reproduction of a single specimen. When FITCH left it was difficult for J. D. HOOKER, who was then editor, to fill his place. However, in 1878 there appeared the first plates from paintings by Miss MATILDA SMITH, and JOHN NUGENT FITCH, a nephew of WILLIAM FITCH, became lithographer. Miss SMITH was a rapid worker and, though her original paintings are often more nearly completed than those of W. J. HOOKER and sometimes those of WILLIAM FITCH, she was in close touch with the lithographer and it was not, therefore, necessary for her to finish the originals to the degree it is now essential so to do with more mechanical methods of reproduction. Miss SMITH contributed the majority of the plates between 1880 and 1920. Two modern gifted artists, Miss LILIAN SNELLING and Miss STELLA ROSS-CRAIG, have maintained, and even enhanced, the reputation of the Botanical Magazine on its pictorial side and their work is still appearing.

Up to 1947, the plates had all been produced by engraving or lithography and the prints hand-coloured. The clear simple washes used by many of the artists, notably by EDWARDS, W. J. HOOKER, and W. FITCH, must have been very helpful to the colourists. In this century it has become increasingly difficult to procure colourists and since the second world war the difficulty became so acute that it was imperative to adopt mechanical methods of colour reproduction if the Magazine were to continue with coloured plates. Both three-colour halftone and photogravure are now being used and experiments with modified collotype have been tried. Many will regret the passing of hand-coloured lithographs but the change was probably inevitable even if it was hastened by post-war circumstances. There is some compensation in that at least as high a degree of accuracy can be obtained in practice by mechanical processes as by hand-colouring. Comparison of different copies of the same plate made by the same or by different hand colourists in the past shows that there was often considerable diver-

gence. Further, certain colours used in earlier days have not stood the test of time and it is reasonable to hope that the modern dyes are more stable. In particular, since photography is the basis of the mechanical processes now used, outlines are very accurate and fine colour markings can be correctly recorded.

In choosing the most suitable plates to illustrate styles, the subjective element naturally enters. It is not possible, in a short space of time, to illustrate the work of all the artists who have contributed to the Magazine. I have, therefore, chosen six and have tried to select as fair examples of their work one or two plates by every one of them. We take them in chronological order:

SYDENHAM TEAK EDWARDS (1769-1822). Almost all of the plates in the first 42 volumes of the Magazine were prepared by this artist. They are remarkable for their finish and accuracy and yet for their grace and simplicity. His method of treating large surfaces of a simple pattern with a single wash facilitated the colourist's task. Complex mosaics of colour were, however, well treated and often beautifully and delicately shown. Examples taken from the original paintings at Kew are *Cercis siliquastrum* (t. 1138) and *Crocus serotinus* (t. 1267).

WILLIAM JACKSON HOOKER (1785-1865). As already mentioned W. J. HOOKER for some years was not only editor and author but artist as well. Many of his original drawings are in pencil with samples of or notes as to colours which were to be added later, probably on an engraving proof. This procedure is well illustrated by the original of *Althaea rosea* compared with the published plate (t. 3198). W. J. HOOKER's drawings show a boldness of composition which is often emphasized in the reproduction process. The drawings themselves are delicate in line and shading and at the same time are accurate and pleasing. The second example of W. J. HOOKER's work, that of *Lonicera hirsuta* (t. 3103) fairly illustrates the same feature. The colours to be added to the engraved drawing are listed on the back of the original. It is probable that the interval of time

between the preparation of the drawing and the receipt of an engraver's proof was often short.

WALTER HOOD FITCH (1817-92). This famous botanical artist was trained by W. J. HOOKER and a study of his original plates clearly shows the influence of HOOKER's style. This influence is evident even in the reproductions especially in their composition. The example of *Cistus vaginatus* (t. 5241) is instructive. The original coloured drawing has one open flower. The uncoloured lithograph, like the finally issued coloured plate shows added flowers in front, back, and side views. The drawing was made in June 1860 and the plate was published about one-third through the volume for 1861. The date of the drawing on stone has not been traced but it was probably some months after the original was drawn and we have here but one of numerous examples of FITCH's retentive memory of details and his power of again visualizing the living plant from his original coloured drawing.

MATILDA SMITH (1854-1926) was trained as a botanical artist by J. D. HOOKER. Her work varied in quality. Some of it was very good especially in arrangement. The example of *Heliamphora nutans* from her original drawing for t. 7093 is a fair sample of mean value. Actually it was well reproduced by J. N. FITCH's skilled lithography.

To conclude examples of plates prepared for the Botanical Magazine, we have slides of originals to illustrate the work of Miss LILLIAN SNELLING and Miss STELLA ROSS-CRAIG. *Gentiana sino-ornata* (t. 9241) and *Ranunculus asiaticus* var. *albus* (t. 9380) by Miss Snelling and *Banksia serrata* (t. 9642) and *X Daphne Burwoodii* (N. S. t. 55) by Miss ROSS-CRAIG show that in all characteristics the modern plates do not fall behind those of past times and that in finish, accuracy and what one may call "vitality" they often show advance in technique.

Something must now be said about the text accompanying the plates. This has changed in form and content more than the illustrations. In the early volumes it is often short and gives little more than the name, a very brief descrip-

tion, a few synonyms, an account of the origin of the material, and suggestions for its cultivation. The descriptions were improved by SIMS and still more by W. J. HOOKER. Minor changes in contents and arrangement were introduced from time to time but the highest standard of text was that set by OTTO STAFF. This editor, like several previous editors, wrote many of the articles himself and the amount of research involved in preparing them was often very great. The consequence is that the Magazine became a medium for the publication of original investigations to a greater degree than ever before and it has been no easy matter for subsequent editors to maintain the general level of scholarship, originality, and taxonomic usefulness of the volumes that appeared between 1922 and 1933. (Only a short differential diagnosis was given in Latin but a very full description in English appeared near the end of every article. The "general talk" was normally much expanded and included a discussion on the taxonomic status of the plant figured, an account of its distribution, and notes on its behaviour under cultivation.)

In the New Series, the publication of which was started in 1948, the following changes in arrangement and matter were made: dissections are entirely and constantly relegated to the text as black and white figures, distribution or range maps are sometimes included, and notes on cultivation are given a separate paragraph title and are usually more detailed. In addition, authors of articles are encouraged to provide more particulars along the lines of the so-called "new systematics" by recording and discussing the ecology, variation, and cyto-genetics of the species figured, so far as data are or can be made available.

What is the present policy of the committee and editor of the Botanical Magazine? Briefly, it may be defined as an attempt to link botany and horticulture more closely together, especially systematic botany in the broad sense and the cultivation of plants for the aesthetic value of their flowers, fruits, and foliage. The aim is to make the Botanical Magazine increasingly

useful both to botanists and to horticulturists. In the choice of plants for figuring attention is given to these two aspects. Only living specimens are figured and such as are in actual cultivation in gardens in the British Isles. Within this restriction we have a wide choice. At Kew alone over 40 000 species of plants are now grown. This number includes trees, shrubs and herbs, as well as hardy plants grown in the open and tender species needing partial or complete greenhouse protection, but it excludes horticultural varieties and hybrids. Granted that not all these species are suitable as subjects for plates in the Botanical Magazine and that many of them have already been figured there is yet a large reserve on which to draw. Moreover, new plants are continually being introduced from floras in all quarters of the globe.

Kew is not the only source of material for the Botanical Magazine. We acknowledge with grateful thanks the help received from the Directors of the Wisley Gardens of the Royal Horticultural Society and of the Royal Botanic Garden, Edinburgh, from the officials of the University Botanic Gardens and of other institutions. Many owners of private gardens have been generous donors as have also firms growing plants commercially.

After careful consideration it has been agreed to depart intentionally from two rules which have been more or less observed in the past. It has been the general practice not to re-figure species of which plates have already been published and not to include hybrids. We intend now to prepare new modern figures of certain species whose earlier representation in the Magazine left something to be desired or about which much more is now known. Also, we have commenced figuring some first generation hybrids, of known ancestry, when these have particular horticultural merits or botanical interest. In the main, however, the plants figured are still to be such as have not previously been illustrated in the Magazine and are the direct result of importations from the wild.

With regard to the accompanying text, it is intended to maintain and to increase the pres-

ent high standard. As far as possible there will be given in outline the known history of the plant figured, its discovery in the wild, and its introduction into cultivation. Its affinities and general systematic position and status will be considered and its name discussed. The botanical peculiarities will be analysed, not only in a full formal description but also in the general text.

Particular attention will be paid to intra-specific variation, geographical range, and ecological behaviour. It is intended to include such details of their genetics as are known and to have the cytology investigated of as many of the actual plants figured as possible. Since voucher specimens of the plants are presented by the Royal Horticultural Society to the Herbarium of the Royal Botanic Gardens, Kew, the inclusion of cyto-genetical data should lead to the gradual accumulation of new verifiable facts to broaden the basis of plant taxonomy.

This brief account of the past and present of the Botanical Magazine will, it is hoped, draw the attention of members of this Congress to its importance to botanists and to all who seek to increase the co-operation between the pure and applied branches of our science. This periodical more than any other represents the systematic side of the "living garden" and botanists and gardeners alike have a duty to support it. In these days of high costs of printing and colour reproduction the Royal Horticultural Society carries a heavy financial burden in connection with the Botanical Magazine. It is essential that its sale should be greatly increased to individuals, botanical institutions, and libraries. The price has not been raised since the devaluation of the pound sterling and there seems every reason for asking all of you to support our efforts to maintain the regular publication of the Botanical Magazine by placing subscription orders with the Royal Horticultural Society, Vincent Square, Westminster, S. W. 1, England. For our part, we will strive to increase its scientific value and its practical usefulness by enhancing its great reputation in both plates and text.

LECTURE 3

Tuesday, July 19th, 8 p. m.

Professor ARNE MÜNTZING, in the chair

Dr. C. D. DARLINGTON,

John Innes Horticultural Institution, Bayfordbury,
Hertford, Herts, Great Britain:

The Study of the Cell in the Understanding of Life

Introduction

We who study plants are concerned to know them with an ulterior purpose: we want to use them, and then to explain them, and finally to control or change them. We have pushed our enquiries to the ends of the earth and to the beginnings of time. We have arranged our material in the finest classification. We have compared the details of structure and of chemical action and constitution as far as our ingenuity will allow. And we have followed our comparison from generation to generation in experimental breeding.

All these studies have revealed order, uniformity or causation. But something is lacking if we are to reach our goals of explanation and control. For this we need to examine the smallest of structures. We could already infer or predict the small structures from studying the large. But much more can we now predict the large from knowing the small. We can predict not only the character of large structures but their action, their behaviour and their evolution,—indeed a large part of the pattern of life.

It was this point of view and this expectation which, during the early part of the 19th century, lay behind the growing idea that all living things at all stages of their growth had a certain common structure: they were divided into units, compartments, or what we call cells. This cell theory had a three fold value: it implied a unity of principle; it directed ideas towards matter, particles and causes and away from forces, humours and purposes; and finally it called for an explanation.

For a long time however, the explanation was lacking. No one could quite see why the cell should be an almost universal unit. To be sure it usually had only one nucleus but this rule could be evaded. It has not indeed been by any facile generalisation but by thorough comparisons and tedious experiments on a great range of animals and plants and their isolated constituents that the meaning of cell structure has gradually—during the period between 1875 and the present day—been revealed. The unity of principle became effective when the study was pushed to a lower level of size than had hitherto been attainable. Similarities of respiration, reproduction, or movement could be noticed without the use of the microscope. But the cell structure seen with the microscope showed a similarity, first of development, then of heredity, and ultimately of molecular organisation.

Cell Physiology

The two main paths of attack on the cell, as on larger structures, are often referred to as the descriptive and the experimental. It is worth discussing on this occasion just how effective and conclusive they are.

The descriptive evidence was clear before 1900. The necessity of a nucleus for the growth of a cell; the continuity of nuclei from one cell generation to the next by mitosis *i.e.* by the formation of chromosomes and their equal division—implying their regular reproduction; the continuity of the chromosomes from one mitosis to the next in the nucleus; the equality of the nuclei in the gametes of sexual reproduction although not of the cytoplasm: all these arguments had been brought forward to show that the nucleus governed the cell and through it governed development and heredity. So that the cell existed as a “sphere of nuclear action”—

to use the same expression that STRASBURGER used in 1893.

The last 50 years have been devoted to clinching the descriptive argument by experiment. Experimentally we may damage the cells of a plant or an animal in many ways, by heat or cold, by chemical agents or by ionising radiations, and in any of these ways we may kill them. But one kind of death alone reveals a process arising from a specific effect of the treatment. If, when the nucleus comes to divide following treatment, one of the chromosomes into which it resolves itself proves to be broken, the fragment will be lost and a daughter nucleus will be formed lacking this piece of chromosome. This daughter nucleus will nearly always sooner or later die. With a small piece of chromosome it loses all hope of posterity.

This principle is most easily seen after X-raying pollen grains, as KOLLER has shown. If it were not true, since breakage and loss in this way occur from time to time in all organisms in the natural course of events, bits of chromosomes would continually be getting lost and the chromosome complement—whose constancy often throughout the history and geography of a species or a genus still excites our admiration—would disintegrate in a few generations.

Thus, not only the nucleus as a whole but the individual chromosomes, even their parts, are indispensable to the life of the cell.

Experimental breeding tells the same story. The whole succession of cells in a healthily developing diploid organism, whether it is pure-bred and fertile or cross-bred and sterile, are themselves viable and vigorous. But after meiosis takes place and the chromosomes are paired and re-assorted the pure bred organism produces healthy haploid germ cells, the cross-bred organism produces a proportion that die: the new combinations of chromosomes do not always work as well as the old ones and the spores containing them are eliminated. This is the cause of sterility.

What does this proportion depend on? A simple rule indicates the cause of death. It concerns the correlation of fertility between

diploids and the tetraploids they give rise to. If diploid plants are infertile it is due to differences between their parents; these differences are evidently carried in their chromosomes since the chromosomes often fail to pair or, when they pair, give rise to new shapes of chromosomes with new combinations of differences. When such diploids give rise to tetraploids by doubling of nuclei, identical chromosomes can pair and fertility is thus restored. On the other hand fertile diploid plants give rise to tetraploids with reduced fertility: in them associations of four chromosomes can be formed and these often segregate into three and one giving germ cells with irregular numbers of chromosomes which die. Thus the proportion of cells which die depends on the proportion with a normal or balanced set of chromosomes; and this in turn depends on the kinds and degrees of differences between the pairing chromosomes and the frequency or regularity of their pairing.

Thus the nucleus (and its chromosomes) must consist of different particles and when it lives healthily its different particles must be acting in a balanced way owing to a correct or adjusted proportion. These particles, since we can see that they are recombined by the crossing over observed between the pairing chromosomes in the mother cell, we define as *genes*, the same genes as those identified by crossing-over in breeding experiments.

How do these genes work? Between adjoining cells there is perpetually either cooperation or competition. They either help or hinder one another. The competition comes to light only when, as we saw, cells differ in chromosome make-up; it expresses itself by the death of the less successful. It is amusing to notice, when some philosophers have proved to their own satisfaction that there is no such thing as competition *within species*, that there is in fact competition *within individuals* and that no organism could itself survive indefinitely without such a rigorous, pervasive, and ever-ready competition. Further the unit of competition, selection, or survival is the cell, the sphere of action of a nucleus. Different spheres of action are sepa-

rated by the barrier or partition of the cell wall. Let us see how this separation works.

A pollen mother-cell undergoing meiosis can easily be ill-treated in such a way that pairs of pollen grains stick together and keep their cytoplasmic connexions. If at the same time the distribution of the chromosomes is upset the nuclei in such pairs of grains are often unequal: one has the chromosomes that fail to get into the other.

In these circumstances the two nuclei should be complementary in a physiological sense, being balanced as a whole, unbalanced and even lethal apart. And BARBER found that in fact they both survive. More than this: both come into mitosis at the same time. Since one would die without the other they are evidently helping one another. And they mark their alliance by a synchronisation of mitosis.

Another situation is that where two nuclei are formed within one cell, one of them being of a tried or normal or balanced type while the other is defective; the defective nucleus will only in extreme cases disintegrate. As a rule it will be carried on by the help of its more efficient companion. As BARBER showed from the synchronised mitoses in orchid pollinia, even single-chromosome nuclei can survive in this way—though for how long we don't know.

Even in different cells good nuclei may help bad nuclei to keep going when the outside supply of materials for growth is abundant, *i.e.* when proteins need not be produced but only consumed. In animal tumours cells with sub-haploid nuclei readily go into mitosis and may multiply indefinitely. In plant root-tips, which are similarly regions of protein consumption rather than production, VAARAMA (1949) has shown that defective nuclei may come into mitosis both in cells of their own and in company with other nuclei. Synchronisation of a pair of nuclei in one cell may fail—probably when one is balanced and the other not balanced.

A variety of relationships therefore seem to occur between cells and nuclei according to their character in four respects:

- (i) the individual competence of the nuclei
- (ii) the complementary or non-complementary genetic outfit of the nuclei
- (iii) the separation of their spheres of action by cell walls.
- (iv) their dependence on their own activity for protein production or otherwise.

Now dissimilar nuclei cooperate. But how do they do so? Each must put into the cytoplasm something which (after due interactions and changes have taken place) the other can take out. There must therefore be an exchange between the resting nucleus and the cytoplasm of those materials which are normally exchanged between genes within one nucleus, an exchange on which the growth and division of the cell depends. This exchange may be very general. Or, as in the case of the synchronised conjugate nuclei of fungi, it may be derived from a particular gene. The physiological interdependence of the allelomorphs of this gene is then made the basis of the mating system of the species. The character of the cell as a unit will evidently depend on the freedom with which the products of the nucleus can diffuse in it and the barriers which restrict this freedom of diffusion with other cells. Whether one or more nuclei work in one unit is of no more account than whether they are diploid or polyploid.

The function of the cell wall in separating *genetically, i.e.* chromosomally, different cells is important after meiosis and also after certain mitotic accidents. Its function in separating *physiologically, i.e.* cytoplasmically, different cells on the other hand is the basis of the whole of development and differentiation. Wherever the cell wall is insufficiently developed, as in the endosperm, or in the pollinia of orchids, cells are carried along together in an undifferentiated synchronised mass. In the extreme case of the orchids the feeble and defective, if there are any, are supported by the healthy. With thick and even with medium walls (*e.g.* in the archesporium of the anther, before meiosis in *Campylocarya*, DARLINGTON and LA COUR 1950) defective cells may fail to survive. The barriers are of

different thickness; the isolation of the cell is of different degrees of intensity.

In dealing with unforeseen genetical accidents a thick wall may be necessary for isolation. For creating a specific adaptive differentiation of two cells with identical nuclei a very tenuous barrier is sufficient. This we see within the pollen mother cell and embryo sac. The differentiation of the materials within these cells is already established, as it is in the animal egg, before any membrane exists (LA COUR 1949). The character of the cytoplasm at the generative pole of the pollen grain (as opposed to that at the vegetative pole) prevents it extracting the nucleotides from the nucleus which is thus left with a high nucleic acid charge. This differentiation determines the different histories of the vegetative and generative nuclei in the pollen grains and presumably of the micropylar and chalazal nuclei in the embryo sac. Both these systems produce a differentiation in the nucleic acid metabolism of the nuclei and their consequent propensity for mitosis. Indeed it seems that in mere degree of *mitophily* we have an elementary and universal basis from which a whole succession of secondary processes of differentiation arise.

In all processes of differentiation where the nuclei are equivalent we see evidence of the cytoplasm telling the nucleus what to do; where the nuclei are not equivalent we see evidence of the reverse. As we saw from the property of cooperation, the relationship must of course always be reciprocal. And it must always be operated by way of the nuclear membrane on whose selective permeability everything else depends.

How can a differentiation arise in a cell without a membrane to protect the differentiated parts?

In a certain sense we may say it cannot. It seems that there must always be some integration of particles capable of long range effects whose surfaces have the properties of membranes if a body of materials is to segregate itself into compartments. This has been very well shown in animals by the experiments of

CLAUDE. It is also shown by the identification of so many visible or deducible particles of genetic continuity, enzyme forming or structure-forming, in the cytoplasm of all organisms, the plastids of plants, the organelles of protista, the centrosomes of plants and animals, the kappa particles of *Paramecium* and so forth (cf. Symposium of the Centre nationale de recherche scientifique, Paris 1949).

We can now take a quick look at a model of the cell as it seems to us to work today. The cell is a sphere of interaction of a nucleus with a body of cytoplasm. On a short view the two interacting elements are of equal importance. The very stability of the nucleus which is ensured by the beautiful accuracy of mitosis prevents its variations interfering in the cell. But on the long view, in heredity and evolution, the stability of the nucleus within the individual makes it the vehicle of long-term changes in the succession of individuals. This vehicle depends for its efficiency on its capacity for recombining differences between chromosomes at meiosis and at fertilisation and thereby exposing them in new forms to natural selection and adaptive evolution.

Apart from the nucleus however there are in the cytoplasm other self-propagating structures capable of change not fully controlled by the nucleus, structures of many degrees of organisation and importance, a hierarchy of particles some of which can intrude into heredity or even infection but most of which obediently serve the nucleus in the short-term processes of differentiation.

The whole cell operates subject to the existence of a variety of selective barriers to diffusion, membranes between cells, nuclei, plastids and perhaps other particles. And between cells there are likewise barriers of different degrees of importance.

Cell Chemistry

With the naked eye we see the growth of plants and animals as due to the formation of new structures. Magnified so that we can see

the cells, growth appears as the formation of different chemical substances, whether a static end-product or a dynamic precursor or enzyme. These substances we are now beginning to relate to the chemical activity of particles visible in the cell, in the cytoplasm as well as in the nucleus.

Apart from nuclear genes there are plasmagenes, plastogenes, genoids, proviruses and even viruses.

Among these particles the first important distinction is between those particles, like genes and plasmagenes, whose activity is adapted to playing a useful part in the life of the cell and those, like viruses and mutant genes of various kinds, which have entered into the life of the cell by infection or mutation and thus have no useful part to play in it. Another important distinction is between those with active and dispersed and those with inert and precipitated products. Many plant viruses appear to differ from normal self-propagating cell proteins merely in producing materials like themselves but otherwise inactive. These inert materials merely distort the life of the cell by filling it up with their own (for the host) useless material, directing the living processes into a blind alley.

The action of a virus can help us to understand the relations of nucleus and cytoplasm. The Severe Etch virus (SHEFFIELD, 1949) causes cell inclusions of two types: mixed amorphous bodies in the cytoplasm which contain the virus itself and protein crystals inside the nucleus. In insects such crystals can include the virus and indeed provide it with a protective shell. It would seem that something absorbed from the cytoplasm with its deranged metabolism has deranged the metabolism of the nucleus so as to produce and accumulate in it quantities of an insoluble protein which, however, have not prevented the continuance of other healthy activities. But what is most significant is that a self-propagating protein, such as is no doubt frequently passing out from the nucleus, can re-enter it from outside. The traffic in genetic particles as well as in other materials is reciprocal. Viruses, we must suppose, arise as

self-propagating cell proteins distinguished from other such proteins by a capacity they acquire and perfect for maintenance by infection. This capacity is now known to exist under artificial conditions in many normal cell constituents which I consequently describe as proviruses. Its high development in incipient natural viruses is probably associated with a second property characteristic of them, namely that of propagation unrestricted by the advantage or survival of the cell into which they have forced an entry.

That is to say, they will multiply beyond the concentration at which they can be useful. It is probably by doing so that they reach a concentration (and an aggregation in particles) at which they can be infectious. Just this change has now been induced by GAUTHERET (1949) by the action of heteroauxin on the tissues of various plants. The action of the changed plasmagene or provirus is recognised by the production of tumours like those arising with Crown Gall from the action of the bacterium *Phytomonas tumefaciens*. Parallel with this change is that produced by grafting where the normal protein of one species or variety is introduced into cells whose nuclei are alien to it and not capable of keeping its propagation within limits (DARLINGTON and MATHER, 1949).

The animal viruses have, many of them, advanced far from what was, on this view, their original character. They have become more complex and are on the way to becoming organisms in their own right. Most plant viruses on the other hand seem to have retained their primitive character. They are probably short-lived in evolution and therefore newer and younger, more like ordinary cell proteins and more frequently able to arise from them. Their study therefore shows us how ordinary self-propagating constituents of the cytoplasm live and work. We find relationships of cooperation, antagonism, mutation, subordination to the nucleus. These properties are less widely demonstrated in animal viruses. But we are able to identify them by breeding tests, in the plasmagenes or hereditary determinants of the

cytoplasm or, by microscopic study, in organelle-forming bodies and microsomes with their attached ribose nucleic acid in the plant and animal cells.

As we have seen, on physiological grounds, the nucleus and cytoplasm must be in continual interaction. It is for this reason that polytene chromosomes of flies vary in visible appearance in different tissues (KOSWIG *et al.* 1947). Similarly MONTALENTI (1949) has shown that the nucleus varies in structure in response to chemical changes in the cytoplasm. The most important of these responses is the entry into division. There are mitosis and meiosis with their endless variations, healthy, and unhealthy. There are also polyteny and endomitosis arising from a modifiable or reversible prophase. Chromosomes vary in size between species and also, in development, within individuals; the cleavage mitoses of animal eggs often have undergrown chromosomes and the antipodal nuclei of plant embryo sacs overgrown ones.

Variation in chromosome size seems to be due to differences in the degree of polymerisation of the chromosomes. Most chromosomes probably exist in a unique transversely polymerised state in which the basic polypeptide chain or monid is multiplied up to 2^{10} or 1024 times. X-raying, which raises the content of cytoplasmic nucleic acid by forcing the nucleus into division in advance of protein supplies, can alter the degree of this polymerisation at mitosis (DARLINGTON, 1950). Mutations have the same effect. We have therefore an environmental, a developmental, and a genotypic means of controlling the polymerisation of the chromosome although the process itself still remains chemically inaccessible.

The high organisation and permanence of the nucleus makes it possible for us to compare the visible actions of particular genes with those of particles outside in the cytoplasm. Our understanding of these matters although rudimentary is already illuminating if we apply the discoveries of CASPERSSON and others on animal cells to our understanding of plants. We have

in the nucleus of most organisms a distinction between two sorts of genes taking part in co-operative activity. First, there are the large and specific genes with large and specific protein products. These make up the *euchromatin* of the chromosomes. Secondly, there are the small and nonspecific genes without individually detectable mutations. These make up the *heterochromatin* which when it is recognisable corresponds with MATHER's polygenes.

All these genes are engaged in producing materials which diffuse inside and outside the nucleus and passing from gene to gene manufacture the important building blocks of development. But there are two other kinds of genes whose products do not diffuse and do not therefore indulge in any indiscriminate cooperation. These are the *nucleolar organiser* and the *centromere*: the economic and the kinetic organs of the chromosomes. Both are compound genes composed by the replication of identical parts. Both are engaged in the secretion, organisation or arrangement of materials whose use to the cell depends on a temporary inertness rather like that of the aggregated plant viruses. The nucleolus, according to CASPERSSON, constitutes a reserve of histone-type proteins and ribose nucleic acid in a semifluid state. The centromere product is the spindle which it organises, sometimes alone, sometimes jointly with the centrosomes in the cytoplasm, bodies which are entirely parallel save perhaps that the centrosomes carry more cytoplasmic, the centromeres more nuclear, nucleic acid. The spindle is a liquid crystal consisting of fibrous proteins organised normally with a perpendicular orientation to these genetic particles. It is capable of being dissolved again rapidly as soon as the daughter nuclei, whose regular separation it has made possible, have been formed. In its origin, structure and stability it is like the flagella of protozoa which are also secreted by genetic particles in the cytoplasm.

Such at least is the superficial account. But between the action of the gene and its visible effects there are no doubt several steps which experiment and comparison can elucidate.

RHOADES has shown that a fluid arising from the centromere can run along the chromosome and, collecting into a drop at the end, proceed to organize a spindle from this temporary site. It is thus evident that the centromere primarily secretes a polymerising or unfolding enzyme, in small quantity, and this enzyme when in contact with the fibre-making molecules of the cytoplasm produces the large scale effect of spindle organisation.

Other properties of chromosomes reflect an influence of the centromere in secreting enzymes (different enzymes concerned probably with nucleic acid) which pass along the chromosome. One is the existence of procentric pairing at meiosis, i.e. the first contact of the pairing chromosomes being near the centromere. Another is perhaps the control of chromosome size revealed in certain circumstances where the genotype is ineffective, e.g. the *Crepis* hybrid of TOBGY where the F_1 chromosomes show the parental differences which are retained for whole chromosomes still even in the F_2 in spite of recombination within chromosomes by crossing-over in the F_1 .

The action of colchicine and other spindle-inhibitors is presumably to inactivate the centromere enzyme. There is also evidence in the work of VAARAMA (1949) of a more profound effect, a permanent change in the centromere itself reducing its effectiveness at the following meiosis, a hypomorphic mutation. Such a parallel effect on an enzyme, and the gene producing it, is of profound interest since, as VAARAMA points out, it could affect the naked centromere although it could hardly be expected to affect the normal nucleotide-protected genes on the condensed chromosomes.

The release by a gene of an enzyme which acts at a distance may also be inferred of the nucleolar organiser. In all cells, or in particular cells of some plants, nucleolar organisation does not take place in the normal way at the specific intercalary organising loci but at the ends of all chromosomes. Here again the enzyme seems to have collected at the end of the chromosome (cf. WOODS, 1937 on *Tulipa*). It may also collect

at the centromere (HÅKANSSON and LEVAN on *Pisum*).

Looking at this problem the other way round we may judge that free diffusion of gene products in the nucleus is probably their common lot; drop diffusion is probably an intermediate situation; and localisation is the rare extreme which enables us to recognise particular kinds of genes—including the heterochromatin when it is recognisable.

The visible action of the centromere again and again confirms physiological principles which have been arrived at by more remote inferences. The processes of differentiation indicate a specificity in the time of action and interaction of genes such as is visibly expressed by the centromeres. They secrete their polymerase only when the chromosomes are spirallised and coated with desoxyribose nucleic acid. Precisely, that is, at the time when all the other genes are precluded from activity. Moreover they are concerned with organising in the spindle a large part of the proteins of the cell, proteins which, many of them, must have arisen through the activity of other genes during previous resting stages. We thus have an example of the reciprocal and successive reactions of nuclear genes and cytoplasmic proteins of which we saw evidence in the matter of the cooperation of defective nuclei. And we begin to see how the converse process of competition is bound to arise through the superior efficiency of a nucleus which has within itself all the genes needed for the succession of transactions with the cytoplasm whose orderly and cyclical sequence maintains the processes of life.

Chromosome Systematics

Cytologists may complain that students of plant life have been slow to apply our analytical understanding of cell processes to problems of the physiology and embryology of plant cells. With genetics and its ancillary disciplines of evolution and systematics the matter is far otherwise. Here none have hesitated to take the plunge in what appeared so safe and shallow

a pool. To conclude the relationship of the parents from the behaviour of their chromosomes in the hybrid, to infer the phylogeny of species and genera from the changes of chromosome number, all the necessary principles seemed self-evident and therefore not worth reciting. But is it so easy as all that?

When we inquire into the problem more closely we find certain notions constantly recurring. The notions of "affinity," "hybridity," "sterility," "genome"—a genome of seven having the specially high mystical name of a "septet"—and finally the "more primitive" and the "more advanced" species.

An analytical approach is more painful. But it is now possible.

In the first place, and above all, we must remember that the chromosomes are not another character comparable with the superficial characters of organisms. The chromosomes determine the characters, the characters do not determine the chromosomes. Changes in the chromosomes determine the isolation and divergent evolution of races, ecotypes, species, and families. Their modes of organisation and mechanisms of recombination at meiosis determine the mating habits of species, the forms of their flowers and the degree of variation that is compatible with their sexual fertility or their apomictic reproduction. And they determine not merely these present properties but all their future expectations. To describe the chromosomes as another "useful character" is therefore not a slight, but a fatal, misunderstanding of the principles of biology.

Coming now to meiosis: We know that the pairing of chromosomes is conditioned by the formation of chiasmata; which in turn is conditioned by the amount of pachytene pairing; which in turn is conditioned by the structural likeness of the pairing chromosomes, by the favourableness or otherwise of the circumambient conditions, by the genotypic character of the organism which may favour one or other system of contact-point, time limit, localisation and so on. We also know, what we might expect, that hybridity is very different in its

effect on chromosome pairing and on fertility according as it is the result of crossing, of mutation or even of selfing; of an F_1 or an F_2 , or a backcross; of structural or of numerical differences between the chromosomes of the parental gametes.

Further, we believe that changes involving the multiplication of chromosome sets are in sexual species irreversible. And the change from sexuality to parthenogenesis likewise. We may suppose that changes in basic number are usually so, increases being so much more frequent than decreases. This one-directional character distinguishes the chromosome number and the properties of meiosis and fertilisation from the super-cellular qualities which are the basis of descriptive classification: it introduces an indispensable frame of reference in phylogenetic considerations.

And again we know that the chromosomes of polyploid species do not live, move, or have their being, in the sets or genomes which we conceive of their having inherited from their remote diploid ancestors. When translocations occur we have no reason to suppose that they take place within sets any more readily than between sets. And when the chromosomes of a diploid species *A* pair with those of a tetraploid of *BC* ancestry we have no reason to suppose that they infallibly pick on either *B* or *C* to pair with. Indeed we know that *B* and *C* may pair together leaving *A* out in the cold. All these reasons lead us to doubt whether the name of a chromosome set has any meaning except a purely numerical one when we are dealing with polyploid species which have undergone evolutionary change since their origin. And when we see such violent changes as FRANKEL has described in an ordinary bread wheat we know that reconstruction is always going on.

There is, however, one more line of reasoning which still deserves to be examined: it is the assumption that one species as such can be more (or less) primitive than another species. The systematist for purposes of classification in any group has to choose one (or perchance two)

of the variable characters of the group as "significant" by which he means convenient. He gets the impression, that variation in this character has been the basis of evolution of the group in question. If the systematist had seen the living plants or animals (which he often has not) this assumption would still be a remarkable one. Often the fallacy is quite obvious. If the tail is the important variable in the *Amphibia* then the tailed Salamander is clearly more primitive than the tailless frog. But, if the method of reproduction is the important variable, then the frog with external fertilisation wins beyond a peradventure. Primitiveness is a function of the character not of the species. At the same time, as we saw, the chromosomes stand apart from all other properties of a species, a law unto themselves. It follows that there is never sufficient reason for supposing from external form that one species has an earlier type of chromosome organisation than another.

There can of course be certain changes in evolution—such as the adoption of parasitism—which dominate all properties of the organism. That is all *phenotypic* properties. But do they dominate the organisation of the genotype? Does the chromosome number necessarily jump when the species changes? Certainly not.

What view does the systematist-cytologist take? He assumes that the allegedly primitive species must have a chromosome number which is itself primitive or original. If this happens to be a high number then evolution has proceeded by a reduction of chromosome numbers. This is a fallacy. Changes of chromosome number are clear and simple and vastly important. But, where the number does not change, its change is obviously not important. And there is no reason to suppose that change of chromosome number is correlated with change in bodily form or function—any more than are changes in two different bodily forms or functions, such as those mentioned in the amphibia. Chromosome numbers, as in species with cryptic polyploidy, can vary without change in external form. And new genera can arise (like *Lolium*

and *Festuca*) without any detectable change in chromosome number or form.

The notion of block primitiveness is like the notion of the block genome. Both depend on the view that the genes all march in step. Both are fundamentally inconsistent with chromosome observations and Mendelian theory which equally demand crossing over. Yet both are put forward by theorists who profess to use these observations and this theory as the basis of their instruction!

The scheme of evolution that we can deduce from chromosome numbers is of obvious importance but its rules have to be laboriously worked out before they can be applied. And they must not be worked out on a foundation of the mythology of old-fashioned systematics.

The most interesting general principle to arise from the study of chromosome numbers in the flowering plants is that which relates the stability of chromosome numbers in groups of species with the longevity of the plants concerned.

There are woody genera, like *Rhamnus*, with more than one basic number of chromosomes. And there are a few largely annual or herbaceous genera, like *Lathyrus*, with only one basic number. But the rule in general is well maintained that woody genera have only one, and woody families no more than two or three, basic numbers. When we turn to the oak, the beech and the chestnut, the pine, the fir and the cedar we find them all testifying their fidelity to the basic number of 12. And in a world of change and flux (as HERACLITUS put it) how can we not admire the stability of the 17 centromeres whose empire, stretching to the limits of the *Pomoideae*, has been undisturbed for fifty million years? Large annual genera on the other hand usually have three or four and often a dozen different basic numbers. Herbaceous and bulbous perennial plants are in general intermediate.

What is the reason for this correlation? That the large and long-lived organism evolves more slowly in form is obvious. But it must change in chromosome number more slowly still. It

evidently cannot afford to experiment so freely as a small short-lived organism (with its much larger populations) in dare-devil and often sterilising novelties such as changes of chromosome number. In consequence the woody flowering plants retain a conservative chromosome structure which reflects their phylogeny often as far back as their origin from non-woody plants and at the same time from a basic number of seven in the primary and secondary geological periods (DARLINGTON and MATHER, 1949). It can therefore be readily related, as JANAKI AMMAL has suggested in *Magnolia*, to the great geological and climatic changes of the tertiary period. Annual and herbaceous plants like *Crocus*, *Crepis* and *Ranunculus*, on the other hand, often cannot be traced even to a common chromosome origin for each genus. Or at best, as STERN has shown in *Paeonia* and elsewhere, they reflect the movements of the Ice Age.

We have thus two speeds of evolutionary change operating for chromosome diversification in terms of phenotypic diversification and illustrating their fundamental distinctness. For the slow-changing woody plants chromosome number is a criterion, the most valuable criterion, of distant relationships. For the rapidly changing annuals it is a criterion of close relationship and its application is to smaller groups.

Among both slowly and rapidly evolving types one of the most remote events that we can deduce with certainty in the history of species is the frequency with which forms with two different basic numbers and sometimes degrees of polyploidy have crossed to give new *diabasic* forms. Take a large woody group and a small annual group of corresponding variability: in the Magnoliales 7 and 12 have evidently united to give 19 while in *Viola* the Old World 6, 10 and 11 have united to give the 27 of the New World. The parents in such cases would differ (and indeed in *Brassica* and *Narcissus* certainly do differ) in an order of discontinuity usually assigned to the separation of species. We have here the evidence of polyphyletic origin in the remote past seen to-day under our eyes.

While we are proceeding by immense surveys of chromosome numbers (in which we hope animal cytologists will soon emulate our success) to trace great evolutionary generalisations we have to remember that it is on the close comparative and experimental studies of changes of chromosome number and structure that we depend for knitting our speculations to the framework of science. The means of restricting crossing-over, the processes of structural change, spontaneous and otherwise, the properties of supernumerary chromosomes, and of their heterochromatin, the modes of centromere reorganisation, these are showing us the physical steps by which the evolutionary panorama is made to unfold. Indeed it has been possible for us to show how the basic number of chromosomes can be raised by centromere breakage and lowered by interchange in one and the same species of *Campanula* (Darlington and LA COUR, 1950).

Perhaps the most striking conclusion about this panorama is the fact now made clear to us that analysis at all the different levels of morphology and chemistry, geography and paleontology, genetics and cytology is necessary to give us the coherent picture we need of evolutionary change. This is true equally whether we consider the detailed problems of the relationships in one small group of species such as those of *Gossypium* or *Paeonia* or great principles and generalisations concerned with the changes of breeding systems and the origins of discontinuities.

Counting the chromosome number is of course only the beginning of what we can learn from the cell for use in classifying a plant or in breeding it. But even this elementary step is not taken in some of our botanic gardens. A large staff is often engaged in providing or changing names for plants by morphological and bibliographic experiments, the chromosome numbers being unknown. Now a chromosome number may be determined in from five minutes to half an hour. It is therefore easy to estimate that four men could in four years count the chromosomes of all the species in a very large botanic

garden. The work involved would represent only a fraction of what is actually undertaken for example at Kew or at the British Museum in the study of dried specimens. Yet the efficiency and reliability of the work done in such institutions would not be doubled or even multiplied by this small addition (or substitution): it would be quite transformed. At present the work of botanic classification is usually uncertain, often ephemeral, and occasionally altogether wrong. Combined with proper chromosome study the results would acquire a new certainty and a new permanence. And occasionally they would be illuminating, not merely to the particular worker, or to the particular problem but to the world and to science at large.

Genetic Embryology

In treating of the bearing of cell studies on the understanding of life I put embryology—the embryology of the flowering plants—last. Not because its present modes of description are the most elaborate, which is no doubt true, but because interactions describable in terms of the chemical, physiological, and genetic notions already touched upon are here all brought to one focus. These different methods of analysis are however all pushed out of view by the two more obvious preliminary methods of treatment, *i.e.* by the formal classification of morphological types of development and their reproductive consequences.

For any one man to hold in his head at the same time all the different considerations that bear on the development of one ovule is perhaps impossible. It is however possible now for us to recognise the scope and function of the different methods of analysis so that each may be put in service in its proper turn. Some of the most favourable conditions for studying how these methods work are found in the development of the embryo sac in the flowering plants. In this field where dead classification and nomenclature have run riot for fifty years we have now (largely through the success of the Swedish

and Italian workers) the comparative and experimental materials for living inference and analysis. We must put out of our heads the time-honoured didactic types and meaningless homologies and consider the genetic and physiological relations of the cells whose development we are reconstructing from the tedious seriation of sections. We then find that one variable is always at work and a second usually at work in controlling the differences of behaviour of the same group of cells. The obligatory variable is the differentiation of the cytoplasm of cells differing in position in any organ such as the ovule. The facultative variable is the differentiation of nuclei appearing in the products of meiosis of all plants or animals which arise from the union of dissimilar gametes. And this differentiation of nuclei must depend for its effect partly on the strength of the cell walls between them.

In the anthers and ovules of the flowering plants a stage is reached in the development of the cells of a central region when they are switched from the mitotic course they have followed up to this point to a new type of cell division, meiosis. The change is connected, as LA COUR has shown, with the supercharging of the resting nucleus with chromosome nucleic acid. This is followed by the onset of prophase before the chromosomes themselves have become susceptible of division (DARLINGTON, 1947).

In the anthers a sharp boundary separates the meiotic cells, the nurse cells, and the ordinary mitotic or mature cells. In the ovule on the other hand a great variety of conditions are found. A single central cell is usually predestined to undergo meiosis. But in many species several adjoining cells enter meiosis together. According to SCHNARF's accounts (1929, 1933) there is what is called a "multicellular archesporium" in 3 per cent of gymnosperms, 6 per cent of monocotyledons, 9 per cent of *Sympetalae* and 25 per cent of *Polypetalae*. Further in particular species or individuals variations occur. In *Oenothera muricata* 12 per cent of ovules contain twin mother cells and later twin tetrads (RUDLOFF and SCHMIDT, 1932).

What does this mean? It seems that some meiosis-determining substance or system of events (related to the observed concentration of nucleic acid) is variable in the extent of its distribution. How it varies is shown where the number of cells is very large. In *Asperula*, with up to 200 potential mother cells, the central cells have an advantage: they are larger and earlier and meiosis is, either regular and gives spores in fours with the reduced chromosome number, or suppressed to give diploid spores which may be fertilised to give triploid embryos. Outside these are delayed cells whose chromosome pairing is incomplete. They give unreduced spores in pairs, which may develop without fertilisation. We then have *diploid parthenogenesis*. Further out still, and still later in development, are cells which go through no pretence of meiosis but nevertheless arrive at the characteristic differentiation of egg and other cells in the embryo sac. They are said to be *aposporous*. And, last of all, cells may develop at the side, without forming any enlarged embryo sac, directly into a *nucellar embryo*. In *Hieracium*, as CRISTOFF found, the breakdown of differentiation may proceed even further, and cells of the integument are pushed over the threshold into meiosis.

In this series we are bound to recognise the same kind of gradient as we found in the pollen grain between the vegetative and generative poles. In one and the same plant, *Leontodon hispidus* (BERGMAN 1935), there are indeed transitions from the level or parallel development of a multicellular archesporium to the steep gradient which leads to the intrusion into the proper embryo sac of a nucellar embryo from the side. Meiosis and fertilisation then fail more frequently as the accessory development grows later and more intrusive.

Such versatile capacities of development are very widespread in the flowering plants. Their morphological classification is arbitrary and formal and serves to hinder the three later modes of analysis which should arise from it. The first of these is the physiological analysis reached when we recognise that different de-

grees of retardation of the accessory cell go with a retardation of the prophase of meiosis pushing it back into a mitotic condition. The second is the chemical analysis reached when we admit that a differentiation, in some cases a gradient, in the distribution of archesporial or meiosis-promoting, and later mitosis-promoting, substances must arise in the cytoplasm of the ovule cells. The third is the genetical analysis which we must now consider.

The results of the coexistence of potential spores in the ovule, some reduced and some unreduced in chromosome number, is bound to be that the unreduced spores will be favoured where the reduction is unsuccessful. The conditions have been shown very well by CHIARUGI in *Artemisia*. If the plant is a hybrid or a triploid, if pairing or segregation is irregular, and if the spores produced are consequently unbalanced or inviable there will be a clonal unreduced spore ready to take the place of the reduced spore and, with or without fertilisation, maintain the production of seed. There will be competition. And this competition will serve the reproductive economy just as competition between normal and damaged mitotic cells serves the vegetative economy. And, whenever a plant matures whose meiosis is wholly unsuccessful, a new and potentially permanent race of obligatory apomict will have arisen. Thus cell competition depending on the makeup of the nucleus is the means of fertility and a device governing the origin of species and the course of evolution, a course which is indelibly recorded by the chromosome numbers of living plants.

The competitive reaction of genetically different potential spores is confused where the ovule contains many meiotic and submeiotic cells by the variable gradients on which they are super-imposed. The situation is simpler where the competition is between the products of one mother cell.

In the Gymnosperms rival egg cells are absolutely predetermined or genetically identical. In the Angiosperms on the other hand embryo sacs containing the egg cells vary in four chief

respects not only between species but often in the same plant:

- (i) In the number of mitotic generations taking place within them.
- (ii) In the gradient of mitotic frequency between the two ends of the embryo sac.
- (iii) In the degree of spindle failure and consequent wall failure and nuclear fusion at the vegetative pole.
- (iv) In the number of spores taking part in them.

Again it has been customary to classify species in series of types according to the effective norm of these four variables in each—or in the individuals examined by the observer. Ranges of behaviour have however been found in genera, species and even individuals. For example one- and two-spore embryo sacs occur together in the same ovule of *Euphorbia characias* (D'AMATO, 1939). These variations not merely indicate evolutionary sequences: they show that interpretation in terms of gradients, subject to genetic and environmental variation is a safer basis of prediction and guide to inquiry than classification by types—a classification which is ideal and scholastic but untrue.

The last two of these variations have important genetic consequences. Normally a triploid endosperm is produced. When triple fusion is reduced a diploid tissue arises. The importance of genetic balance for the development of the endosperm and hence of the embryo has been shown by HIORTH (1928) in *Oenothera* hybrids. The fact that *Oenothera* has a diploid endosperm must thus underlie the development of balanced complexes in this genus and it is remarkable that the other notable ring forming plant *Rhoeo discolor* has triploid endosperm (MULDAL 1948).

The formation of endosperm with 4, 5 or even 14 chromosome sets must also have special adaptive and evolutionary consequences. It is at once obvious for example, that fusion of chalazal nuclei occurs only in 4-spore embryo sacs and thus, where it is regular as in *Fritillaria*, it removes the dangers of inviability by

undoing segregation: it saves eggs. In *Tulipa* of the *Leiotemones* section similarly it is not surprising that fusion which is usual in the diploid species is omitted in a pentaploid. The chromosome character of the plant is bound to condition adaptively the mode of development that the endosperm follows.

The most critical information of genetic interest, however, arises from the single-spore embryo sac. In determining which of the four spores shall develop, no doubt, a physiological gradient is usually of predominant importance. Hence No. 4 is predestined to develop in the Normal type, No. 1 in *Oenothera* and *Rosa*, and No. 3 strangely enough in *Aristotelia*. But, in his critical experiments with *Oenothera*, RENNER was able to prove that other embryo sacs could replace the physiologically favoured one if that one was genetically disfavoured as a result of segregation at meiosis.

RENNER thus discovered two principles at once: a genetic competition between cells and also a competition between genetical and physiological differentiation in determining the development of cells. This principle of the RENNER Effect may be seen to act in a hundred other genera in which the predestination of the embryo sac, from SCHNARR's account (1929), is said to vary. Another way of obtaining the same result arises with many-spored embryo sacs as in *Leontodon* where one, three or all four of the spores may take part with a success depending, in part, no doubt on the relative viability of the products of segregation, and in part (recollecting BARBER's experiment) on the degree of breakdown of the cell walls between them. Indeed it seems likely that all flowering plants which, being heterozygous and segregating, produce dissimilar spores are capable of allowing a more viable to supplant a less viable one and so assist fertility.

With the RENNER Effect and all we know of pollen development in hybrids in view, it is impossible to doubt that the same principle of competition acts as between all the other rival potential spores, embryo sacs, and embryos, sexual, parthenogenetic and vegetative arising

within the same ovule. And when any of these competitors are sufficiently equal to allow both to survive we have fraternal twinning or polyembryony, identical twins arising, of course, as in many animals from mere cleavage of embryos. If the frequency of fraternal twins is an indication of equal competition how much more frequent must be unequal competition which gives the single seedling, sexual or apomictic, as a product of natural selection!

Plant embryology thus offers us the most intricate problems of cell-study. When we can effectively bring the physiological, chemical, and genetic interpretations to bear on these problems we shall have the means of acquiring a new understanding of the working of the cell also and of the evolution of plants.

The Causal Framework of Plant Science

I have attempted to sketch the observations and ideas which are arising from the study of the cell and are enabling us to establish a unified plant science. The basic of this unity is the causal connexion gradually established in this century between the particles of the nucleus and the properties of heredity, a connexion first implied by the great Mendelian hypothesis, the hypothesis not of segregation but of determinants. Step by step—always assisted by study of the cell—this hypothesis has advanced. From covering heredity in the chromosomes it has extended to their variation, adaptation and evolution. From treating of the repetition of differentiation in successive generations it is beginning to explain differentiation itself. By showing us the rigid and permanent structure and habits of the nucleus it has enabled us to approach the more evasive properties of the cytoplasm which are responsible for their differentiation. By revealing the analogous chemical basis of self-propagation, the nucleoproteins, in the cytoplasm and in the nucleus, it has shown us their complementary work in the organisation of life. It has shown us the points where development, heredity, infection and

evolution meet and interact. A simple hypothesis has grown to be great central framework of plant and animal science.

All this is only a beginning. But its momentous implications have to be understood if we are to surmount the obstacles of the future. These are of two quite different kinds.

On one side there is the chemical obstacle. For establishing the physical foundations of our subject we have to wait for a better understanding of the chemistry of proteins and of their combinations with the other families of molecules. Such great problems as that of the subdivision of the chromosome into its ultimate polypeptide units or monids can be ultimately resolved only by physico-chemical techniques.

On the other side we have the descriptive obstacle. The older branches of botany (and zoology) have developed as formal systems which stand inevitably opposed to the analytical methods of genetics and cytology. Systematics, morphology and ecology have all reached a point where they can move no further without the help of the analytical methods and deterministic principles which are embodied in the causal framework of genetics. Yet these methods and principles are difficult to those who have not grown up with them. Long chains of causation discovered by inference and conjecture are uncongenial to those who follow the customs of descriptive science. Rather than adopt them we see them turn rather to repetition. Sometimes even they defend themselves with elaborations of bibliography and with making names which cause confusion instead of providing its remedy. I venture to think, however, that the time is not far distant when even the most venerable botanical institutes and gardens will require their staffs to emerge from their herbaria and to study and to name the living plants in their own collections and, in order to do so correctly, will permit the bagging of flowers for experimental crossing and will take the final fearful step of using the microscope in the study of the cell, as a necessary preliminary to the use of the pressed specimen in the classification of the species.

Summary

The central problems of Life are those of growth, and reproduction, and heredity, of variation, evolution and classification. Whatever we know of these from their large scale manifestation we can infer nothing of the minute processes which underlie them. From these minute processes, however, we can infer a great deal of the large scale consequences. Indeed the minute processes, we now learn, determine these consequences and enable us to predict them. Without the understanding of the small determinants in the cell (ultimately in terms of physics and chemistry) the large consequences appear as a labyrinth whose paths we may trace and retrace without finding the way out. The clue to the way out is revealed to us by the microscope with observations that can be repeated and with predictions that can be verified and applied to the extension of knowledge.

The present study is accordingly an attempt to consider the physiological character of cells, its determination by the interaction of nucleus and cytoplasm, the relations of infective and hereditary particles, the chemical activities of genes visible in the cell, the properties of balance, cooperation and competition, and the bearing of the principles induced on embryology, development and classification.

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LECTURE 4

Tuesday, July 19th, 8 p. m.

Professor M. G. STÄLFELT, in the chair

Dr. VALE VOUK,

Professor der Botanik an der Universität,
Zagreb, Jugoslavien:

Die Probleme der Biologie der Thermen im Lichte der neuesten Forschungen

Meine Damen und Herren!

I

Bevor ich an das eigentliche Thema herangehe, kann ich es nicht unterlassen, an jenen Mann der Linnéischen Klasse „Patres Botanices“ zu erinnern, der eigentlich als erster die seltsamen Blaualgenpflanzen aus dem heissen Wasser beschrieben hat. Dies war CARL ADOLF AGARDH, der schwedische Altmeister der Algologie, der sich im Jahre 1826 auf einer

Reise nach Venedig zwei Wochen in dem damals österreichischen Kurorte Karlsbad (Karlovy Vary) aufhielt und bei dieser Gelegenheit die ersten Algen aus dem heissen Wasser beschrieb. Die wissenschaftliche Mitteilung darüber erschien unter dem unauffälligen Titel: „Aufzählung einiger in den österreichischen Ländern gefundenen neuen Gattungen und Arten von Algen“ in der damals führenden Regensburger Flora (1827). Einige Jahre später erschien auch AGARDHS grundlegende Arbeit „Des Conferves thermales de Carlsbad“ (1834). Die Entdeckungen des schwedischen Forschers über pflanzliche Wesen im heissen Sprudelwasser müssen in der damaligen wissenschaftlichen Welt grosses Aufsehen erregt haben, denn kurz darauf folgten weitere Forschungen über die Lebewesen in Thermalquellen, so jene vom be-

kannten Prager Naturhistoriker CORDA, der einige Abhandlungen (1834/5) „Über mikroskopische *Animalcula*“, schrieb, weiters jene vom Begründer der Mikrobiologie FERDINAND COHN, der bereits die Beziehungen der Thermalalgen zur Bildung des Sprudelsinters erkannte (1826), und namentlich jene des italienischen Algologen MENEGHINI über die Algenwelt der bekannten Eugannäischen Thermen (1837–1844) in Italien. Es ist nicht meine Aufgabe, hier weitere historische Reminiszenzen aus dieser ersten *floristischen Epoche der Thermalbiologie* anzuführen, da darüber in der speziellen Literatur bereits berichtet wurde (ELENKIN, EMOTO). Es reihten sich Berichte aus den verschiedensten Teilen der Erdoberfläche über das Leben nicht allein der Pflanzen, sondern auch der Tiere in warmem und heissem Wasser in solcher Folge an, dass im ersten Jahrhundert der Forschung deren Zahl auf mehr als zweihundert anwuchs. Alle diese Abhandlungen hatten mehr oder weniger den Charakter der „Curiosi-Botanik“, da sie in erster Linie „*vegetabilia rara proposuerunt*“ und erst in zweiter Linie auf die Kuriosität des unter den hohen Temperaturen sich entfalteten Lebens aufmerksam machten. Durch die Fülle von Beobachtungen schimmerten jedoch allmählich immer deutlicher rein biologische Fragen hindurch, die zum ersten Male von mir im Jahre 1923 in einem Vortrage gelegentlich der Jahrhundertfeier deutscher Naturforscher und Ärzte, betitelt: „*Die Probleme der Biologie der Thermen*“, zusammengefasst worden sind. Es dürfte kein Zufall sein, dass daraufhin einige der bedeutendsten Untersuchungen über diese sonderbaren Mikrobiotope und ihre spezifischen Biozönosen folgten.

Dass sich an der weiteren Erforschung der „umraumfremden Quellen“, wie sie G. H. SCHWABE treffend nannte, überwiegend Botaniker beteiligten, darf nicht wundernehmen, da die dominierenden Bewohner dieser Biotope in der ersten Linie Pflanzenorganismen, und zwar aus der Gruppe der auf der niedrigsten Stufe der Entwicklung stehenden Blaualgen sind. Von den allerwichtigsten Untersuchungen dieser neueren Periode nenne ich zunächst die folgen-

den: jene von VILHELM in der Tschechoslowakei (1924), von MOLISCH über die Lebewelt der heißen Quellen in Japan (1926), von VORONICHIN im Kaukasus (1926), von FAMIN in Frankreich (1931), von GETTLER und RUTTNER im Sunda-Gebiet in Ostasien (1936), von COPELAND in Yellowstone (1937) und namentlich von G. H. SCHWABE in den Urländern der Thermalquellen auf Island, in Japan und in Chile (1933–1940). Es folgten auch Zoologen mit Forschungen über die Tierwelt in Thermalquellen, von denen einige besondere Beachtung verdienen, wie jene von BRUES über Thermen in USA (1924–1933), von PAX in Deutschland (1932–1942) und die letzten von TUXEN auf Island (1944). Schliesslich fehlten auch nicht Versuche einer synthetischen und vergleichenden Bearbeitung des vorliegenden Untersuchungsmateriales (ELENKIN 1936, VOUG 1937, SCHWABE 1942); doch eine komplette biologische Monographie über die gesamten Probleme blieb bis heute noch aus, obwohl bereits klar geworden ist, dass die Lösung dieser Probleme nicht allein für die allgemeine Biologie, sondern auch für die Anwendung im Leben des Menschen von nicht zu unterschätzender Bedeutung ist. Thermalquellen werden bekanntlich seit Jahrtausenden als Heilquellen benützt. Die letzten Jahrzehnte der Forschung auf diesem Gebiete haben aber gezeigt, dass die wissenschaftliche Bäderkunde, die Balneologie, sich in mancher Beziehung auf die Biologie stützen muss, wie dies in meiner dieser Tage erschienenen zusammenfassenden Schrift, betitelt „*Ein Grundriss zur Balneobiologie*“, zu zeigen versucht worden ist.

Ich benütze nun die Gelegenheit dieser internationalen Versammlung interessiertester Biologen, um auf die eigentümlichen, wichtigen, doch meistens ungelösten Probleme der wirklich „kuriosen“ Biotope hinzuweisen und zu zeigen, wie — um mich der Worte SCHWABES zu bedienen — „diese winzigen Inseln mit Durchmesser von ein Paar Schritten kostbare Laboratorien sind, in denen unzählbare Versuche ablaufen und in jedem Augenblicke neue angesetzt werden“.

Es ist selbstverständlich, dass in der kurz

bemessenen Zeitspanne, die mir zur Verfügung steht, nur die Möglichkeit gegeben ist, auf die zu lösenden Probleme hinzuweisen, ohne ihnen auf den Grund zu gehen. Nicht mehr und nicht weniger ist der Zweck dieses Vortrages.

II

Die ersten Fragen, denen wir bei der Betrachtung eines thermomineralen Biotopes begegnen, sind die *Besiedlungsfragen*, d. h. die Fragen der biotischen Zusammensetzung der Besiedlung in qualitativer und quantitativer Hinsicht sowie der Herkunft der Besiedlung.

Alle bisherigen Erforscher der thermomineralen Quellen sind einstimmig in der Konstatierung, dass als typische und charakteristische Bewohner dieser warmen und heissen Biotope an erster Stelle Blaualgen stehen. Man kann allgemein sagen: *die Blaualgen gehören zu dem Begriff einer Therme im biologischen Sinne*. Sie überwiegen in der Besiedlung wie in qualitativer so auch in quantitativer Hinsicht. An der Blaualgenvegetation beteiligen sich hauptsächlich Arten hormogonaler und chroococcaler Gruppen. Von hormogonalen *Oscillatoriaceen* überwiegen die Gattungen *Oscillatoria* und *Phormidium* und von den *Chroococcaceen* die Gattungen *Chroococcus*, *Gloeocapsa* und *Synechococcus*. Um ein statistisches Beispiel der Zusammensetzung der Blaualgenvegetation zu geben, erwähnen wir die quantitative Zusammensetzung der Blaualgenflora von Yellowstone nach COPELAND. Diese Thermalfloora besteht aus 48 Gattungen der *Cyanophyceen*, die mit 166 Arten vertreten sind. Die meisten Gattungen sind mit 1 oder 2 Arten, hingegen die Gattung *Oscillatoria* mit 22 und die Gattung *Phormidium* mit 19 Arten vertreten. Den *Oscillatoriaceen* am nächsten kommen der Artenzahl nach die *Chroococcaceen*, und zwar *Synechococcus* mit 16, *Gloeocapsa* mit 10, und *Chroococcus* mit 9 Arten. Insgesamt sind die *Oscillatoriaceen* mit 25 % und *Chroococcaceen* mit etwa 20 % an der Gesamtzahl von Arten beteiligt. Es gibt auch Ausnahmefälle, in denen die Blaualgen quantitativ andere Algen nicht überwiegen, wie das oft der Fall ist bei niederen Temperaturen oder in spezifischen Mi-

neralquellen, in denen spezifische Mineralstoffe auch spezifische Biozönosen bedingen, so z. B. in gewissen Schwefel- oder Eisenquellen.

Die Blaualgenvegetation ist hauptsächlich durch den Temperaturfaktor und verhältnismässig niedrigen Salzgehalt bedingt. Vergleichende Studien, die wir seinerzeit über 40 verschiedene Thermalquellen von verschiedenen Kontinenten und Ländern durchgeführt haben, ergaben u. a., dass in den Thermen die *Cyanophyceen* gegenüber *Chlorophyceen* samt Konjugaten im Verhältnis von 62:14 stehen. *Diatomeen* kommen in grösserer Anzahl in einigen silkatreichen Quellen oder auch kochsalzreichen Quellen vor, wo sie scheinbar die Hauptcharakteristik bilden, doch sind solche Quellen, wie die Beobachtungen gelehrt haben, in der Regel irgendwie mit dem Süsswasser in Kontakt (Randquellen, Mischquellen). Thermophile Formen der *Diatomeen* sind bisher nur selten beschrieben worden, wie *Nitzschia thermalis*, *Pinnularia viridis*, *P. appendiculata* und *Navicula cryptocephala*. Eine Massenvegetation der Diatomeen in Thermen, wie z. B. *Pinnularia* in Masutomi in Japan, ist sehr selten. *Desmidiaceen* sind in Thermen sehr sporadisch beobachtet worden und sie stellen im allgemeinen wie die Diatomeen thermoxene Elemente dar.

Was Bakterien als Bewohner der Thermen betrifft, die eigentlich, was die Temperatur anlangt, sogar den *Cyanophyceen* überlegen sind, muss man sagen, dass sie im allgemeinen bisher systematisch wenig untersucht worden sind. Die Bodenschlamm Bakterienflora in Thermen ist nur in einigen Fällen untersucht worden, wobei spezifische thermophile Bakterien entdeckt worden sind (KARLINSKI, GEORGEVITCH, WITTLIN u. a.). Viel besser sind Bakteriengruppen untersucht, die dem spezifischen Chemismus der Thermen angepasst sind, so z. B. die Gruppe der Schwefelbakterien, Eisenbakterien, der kalkablagern und kiesel-speichernden Bakterien. Die verschiedenen Gruppen der Schwefelbakterien (schwefelwasserstoffoxydierende *Leucothiobakterien*, autotrophe *Rhodobakterien*, schwefeloxydierende *Thiobazillen* und sulfatreduzierende

de Formen), die im Grunde genommen keine typischen Thermalorganismen sind und in der Regel in Hypothermen vorkommen, sind die am besten bekannten und untersuchten Formen. Sie kommen oft in Massenvegetation vor und geben einigen Thermalquellen den Charakter, so verschiedene *Thiothrix*-Arten, und namentlich die von MIYOSHI entdeckte „Schwefelrasenbakterie“ in einigen japanischen Thermalquellen. Diese wurde später von MOLISCH beschrieben, aber nicht näher untersucht. Wir (VOUK und Z. KLAS) haben diese seltsame Massenbakterie unlängst in einigen makedonischen Thermen Jugoslawiens (Katlanovo, Kosovrasti und Debar) entdeckt. In dem Namen „Schwefelrasenbakterie“ (wir nennen sie *Thiopoabakterien*) sind wahrscheinlich verschiedene Arten inbegriffen, die in rasch fliessenden Schwefelthermen am Boden der Abflüsse milchigweisse, schleimige, am Rande zerfetzte Lager bilden, die aus zoogloa-artigen Bakterienmassen bestehen. Diese Bakterien sind bisher weder morphologisch noch physiologisch analysiert worden. Wir vermuten, dass es sich um autotrophe Bakterien handelt, deren Studium interessante Resultate verspricht und unserer Ansicht nach für das Problem der Herkunft des Lebens in Thermen von grosser Bedeutung wäre. Überhaupt soll die Notwendigkeit betont werden, dass sich in Zukunft an der biologischen Erforschung der Thermen nebst Alologen auch Bakteriologen viel mehr beteiligen.

Was die Tierwelt im Thermalwasser anlangt, so gehören deren Vertreter den verschiedenen Gruppen der hydrobiontischen Tiere an, die sonst allgemein in gewöhnlichen Süssgewässern verbreitet sind und sich allmählich an höhere Temperaturen der Thermalquellen angepasst haben. Darin sind alle Tierforscher der Thermalquellen (BRUES, ISSEL, PAX, TUXEN u. a.) einig. Wichtig ist die Feststellung TUXENS, dass die Tierwelt der Thermen fast ausschliesslich aus herbivoren Arten besteht. Sie besteht hauptsächlich aus Insektenlarven (seltener Imagines), Mollusken, einigen *Crustaceen* und Rotatorien noch bei Temperaturen bis etwa über 50° C, des weiteren aus Vertretern von Proto-

zoen, Nematoden, Anneliden, Amphibien und sogar auch einigen Fischen, die meistens den Temperaturen unter 40° C angepasst sind. Die Biologie der Tiere hat auch gewisse spezielle Probleme, auf welche neuestens TUXEN aufmerksam machte, auf die wir aber hier nicht eingehen können.

Auf Grund der Kenntnisse über die Zusammensetzung der Besiedlung der Thermalquellen hat man schliesslich versucht, sie zu klassifizieren und typisieren. Solche Versuche, eine Typologie der Thermalquellen auszuarbeiten, hatten den Zweck, eine allgemeine Charakteristik der Thermen zu geben, die eventuell der praktischen Balneologie dienen könnten. Wir konnten allgemein nach den dominierenden Organismen einige Haupttypen unterscheiden wie: Blau-Thermen, Blau-Kiesel-Thermen, Blau-Grün-Thermen, Schwefel-Blau-Thermen, Schwefel-Thermen. Unabhängig von uns hat auch SCHWABE folgende Grundtypen unterscheiden können: Blaualgenquellen, Kieselalgenquellen, Grünalgenquellen, Schwefel- und Eisenbakterienquellen. Von Blaualgenquellen konnten wir bereits drei Untertypen (*Mastigocladus*-, *Oscillatoria*- und *Phormidium*-Typus) und SCHWABE nach Erfahrungen in Japan, Chile und Island sogar sieben Typen (*Cyanidium*-, *Mastigocladus*-, *Synechococcus*-, *Calothrix*-, *Oscillatoria*-, *Nostoc*- und *Misch*-Typus) unterscheiden. Diese Typenlehre ist zur Zeit auf der floristischen Grundlage aufgebaut und in der Zukunft soll der Standpunkt der Ökologie bzw. Zönologie mehr berücksichtigt werden.

III

Es ist selbstverständlich, dass in der ökologischen Forschungsrichtung, die auf die floristisch-systematische folgte, der Temperaturfaktor mehr oder weniger einseitig, wie sich SCHWABE ausdrückt, überbetont wurde. Selbst das äussere Bild der Vegetation einer Thermalquelle wechselt je nach der Temperatur. Im Anfang der Erforschung des Lebens in Thermalquellen interessierten sich die Biologen zuerst für die obere Temperaturgrenze, bei welcher das Leben noch möglich ist. Die ersten Mitteilungen

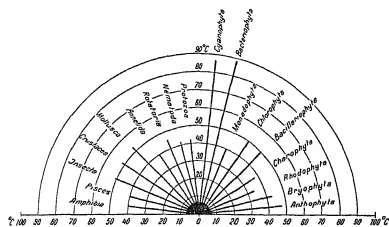


Abb. 1. Bildliche Darstellung der oberen Temperaturgrenze des Lebens für das Vorkommen der Organismen in Thermalquellen. (Nach Angaben von COPELAND; Originalzeichnung.)

waren oft erstaunlich, aber auch widersprechend. Man findet noch immer in biologischen Werken die ältesten phantastischen Angaben von FLOWERS und BREWER, nach welchen lebende Algen bei einer Temperatur von über 90°C beobachtet wurden. Diese, wie auch die neuere Mitteilung von VILHELM (1926), nach welcher in der Therme Piešťany in der Slowakei die Alge *Symploca thermalis* bei einer Temperatur von 93°C beobachtet wurde, erwiesen sich als übertrieben und unrichtig. Dagegen wurden die älteren Angaben amerikanischer Forscher (DAVIS, WEED, WEST) über die höchste Temperatur von 85°C für Blaualgen in Yellowstone neuerlich von COPELAND durchwegs bestätigt. Für Bakterien unbestimmter Art gibt COPELAND sogar die höchste Temperatur 88°C. Ich selbst habe am Rande einiger Geysire in Yellowstone, wo noch Algen lebten, allerdings nur 69°C verzeichnet. MOLISCH hat in japanischen Thermen als höchste Temperatur für das Leben der Algen dieselbe obere Grenze von 69°C bestimmt, und unlängst konnten wir wieder im jugoslawischen Makedonien in der Therme von Strumica die oberste Temperaturgrenze für lebende Algen mit 67°C verzeichnen. Diese Thermalquelle hat an ihrem Austritt die Temperatur von 73°C, jedoch ist zwischen 73°C und 67°C die Quelle vegetationslos. Einen noch interessanteren Fall konnten wir in der serbischen Therme Vranja beobachten. Am Austritt einer Therme war eine Temperatur von sogar 92°C zu verzeich-

nen, doch die Vegetation der Blaualgen war im Gebiete dieser Thermalquellen nur bis zu 56°C entwickelt. Diese Verschiedenheit im Verhalten der Blaualgen zu hohen Temperaturen in verschiedenen Thermen ist uns zur Zeit unverständlich. Andererseits wurde konstatiert, dass ein und dieselbe morphologische Art wie *Mastigocladus laminosus* in verschiedenen Thermen verschiedene Maxima erreicht. Diese verbreitetste Art der reinen Akrotothermen erreicht das Maximum von 56°C. Doch wurde dieselbe Art von ELENKIN in Thermen von Kamtschatka bei 73°C und von uns in Makedonien bei 67°C beobachtet. Es scheint also, dass das Optimum für das Leben dieser Alge beweglich ist, d.h. mit anderen Worten, dass es in Bezug auf die Temperaturresistenz physiologische Rassen gibt.

Was die obere Temperaturgrenze der Blaualgen und Bakterien im Vergleiche zu allen anderen Organismen anlangt, verblüfft uns gerade die Tatsache, wie diese Organismen den anderen überlegen sind. Der Blick auf das Graphikon (Abb. 1) zeigt uns diesen krassen Unterschied zwischen der Gruppe der *Schizophyten* (Akaryonten) und allen anderen Organismen. Die hohe Temperaturresistenz oder Anpassungsfähigkeit an hohe Temperaturen gehört jedenfalls zu einer physiologischen bzw. ökologischen Charakteristik dieser Organismengruppe.

Aus dem beiliegenden Schema der Temperaturbeziehungen lassen sich leicht drei Gürtel oder Stufen unterscheiden:

- 1) die höchste Stufe der Blaualgen, die bis zur Temperatur von über 80°C reicht (die Stufe des heißen Wassers),
- 2) die mittlere Stufe der Grünalgen und Diatomeen, die durchschnittlich die Temperatur von 50°C kaum oder selten überschreitet (die Stufe des warmen Wassers). Dieser Stufe gehören auch bestimmte Tiere: Mollusken, Krustaceen und Insekten, an, und
- 3) die unterste Stufe der Monodophyten und Charophyten (von Tieren Protozoen und Rotatorien), die in der Regel die Temperatur von 40°C nicht überschreiten.

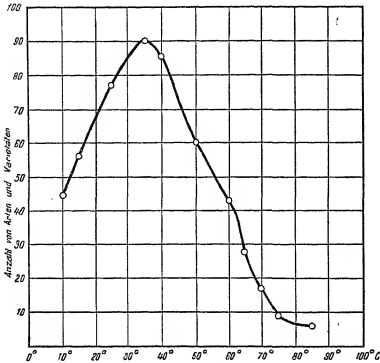


Abb. 2. Die quantitative Verteilung von Blaualgen bei verschiedenen Temperaturen in Thermalquellen im Yellowstonegebiet (USA.).

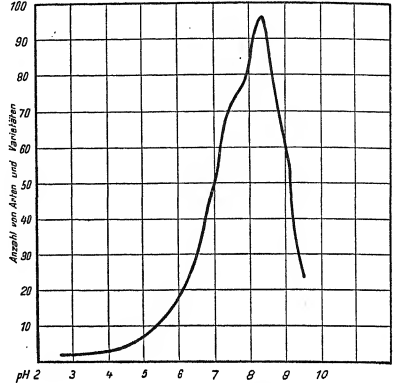


Abb. 4. Quantitative Verteilung der Arten von Blaualgen in Beziehung zur Wasserstoffionenkonzentration im Yellowstonegebiet. (Nach Angaben von COPELAND.)

Die Blaualgen sind jedenfalls sehr eurytherm' und zwar mesoeurytherm, da das Optimum ihres Vorkommens zwischen 30° und 40° C fällt, wie dies die beiliegende Kurve (Abb. 2) der quantitativen Verteilung von Blaualgen in Yellowstone, aufgestellt nach Angaben von COPELAND, zeigt. Um eine richtige Einsicht in Temperaturverhältnisse und Beziehungen zu gewinnen, wäre es zunächst notwendig, die Temperaturvalenzen für einzelne Blaualgen experimentell festzustellen. Die Intensivierung der ökologischen Arbeit in dieser Richtung wird uns gewiss auch besseren Einblick in die bis-

herigen Bemühungen, eine Klassifikation der Thermalquellen nach dem Temperaturfaktor aufzustellen, erlauben. Die bisherigen Klassifikationen (HANSRIG, VOUG, ELENKIN, STROUHAL) haben uns nicht befriedigen können. Erst die Anwendung der ökologischen Valenzlehre (VOUG), die in erster Linie das Optimum berücksichtigt, hat uns die Möglichkeit gegeben, diese Verhältnisse klar zu fassen. Wir bekommen dadurch eine zufriedenstellende Aufteilung der Organismen in Psychrobionta und Thermobionta mit der relativen Grenze von 25° C. Das beiliegende Schema (Abb. 3) soll uns als Grundlage bei künftigen ökologischen Forschungen dienen.

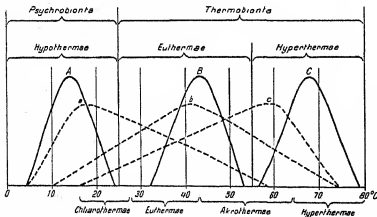


Abb. 3. Die schematische Darstellung der Anwendung der ökologischen Valenzlehre auf die biologische Klassifikation der Thermobionten.

Was andere ökologische Faktoren, wie Wasserstoffionenkonzentration, Sauerstoff- und Kohlensäuregehalt, Licht, Wasserbeweglichkeit, Relief der Quelle u. a., anlangt, so kann man heute sehr wenige Angaben vorlegen.

Die Wasserstoffionenkonzentration („pH“) des Thermalwassers wurde bereits in einigen Arbeiten neueren Datums (FAMIN, COPELAND, TUXEN, SCHWABE) berücksichtigt. Im allgemeinen kann man sagen, dass das Leben der Blaualgen in thermomineralen Wässern alka-

lischem Medium angepasst ist. Das Kurven-diagramm (Abb. 4), nach Copelands Beobachtungen konstruiert, zeigt das Optimum der Verteilung der Blaualgen zwischen pH 8-9, das gegen 7 stark abfällt. Es gibt nur wenige bisher bekannte streng azidophile, mikrostenonische Arten, wie z. B. *Phormidium acidophilum* oder die seltsame Art *Pluto caldarius* (nach GEITLER *Cyanidium caldarium* genannt), die in japanischen Thermen (Kusatsu, Yumoto, Nakabusa) und ebenso in einigen chilenischen Thermen (Ramuncho, Takahuaano, Zapallar) an pH 6 gebunden ist, aber auch pH 2,6 verträgt. Es wäre eine dankbare Aufgabe, diesen noch rätselhaften Organismus einer eingehenden ökologischen Analyse zu unterziehen.

Was den Kohlenstoffsäuregehalt anlangt, der in einigen Hypothermen auch einen grösseren Grad (bis zu $0,7 + 1,2 \text{ CO}_2$ pro 1 l.) erreicht, so fand BRABETZ in dem Thermalgebiete von Mariánske Lázně (Marienbad) in der Tschechoslowakei, dass einige Blaualgen an den reicheren Gehalt der freien Kohlensäure angepasst sind. *Oscillatoria tenuis* könnte sogar als CO_2 -Indikator in Mineralquellen bezeichnet werden. PRÁT hat in anderen tschechoslowakischen CO_2 -Quellen eine neue Blaualge unter dem Namen *Oscillatoria carboniciphila* beschrieben, die ebenso an den höheren Gehalt von freier Kohlensäure angepasst ist. Immerhin scheint solche Anpassung selten zu sein.

Der Sauerstoffgehalt befindet sich in thermalen Quellen an ihrem Ursprungsorte im Minimum. Bei 50°C sind die Thermalquellen beim Austritte aus der Erde eigentlich als sauerstofffrei zu bezeichnen. Nach TUXENS Beobachtungen in Island steigt der O-Gehalt sichtlich mit der Entfernung von der Austrittsstelle. Von $0,48 \text{ mg/l}$ bei 48°C am Austrittsort der Quelle, steigt der Gehalt an O bei 11 m. Entfernung vom Austrittsorte bis auf $5,58 \text{ mg/l}$. Die Thermalalgen scheinen an sehr geringen Sauerstoffgehalt angepasst zu sein.

Die Beziehungen der Thermalalgen zu den verschiedenen mineralischen und gasartigen Stoffen, die oft in grösserer Menge in Thermen

vorkommen, sind bisher so gut wie gar nicht untersucht worden. Hier liegt ein weites Untersuchungsfeld namentlich für Physiologen vor. In der ersten Linie interessieren uns natürlich die biogenen Elemente N und P. Auch die Beziehungen zu der Gesamtmenge mineralischer Bestandteile sind uns unbekannt. Damit in Beziehung steht die in Thermen oft vorkommende Erscheinung der Sinterbildung (Kalk- und Kieselsinter). Inwieweit diese Erscheinung mit dem Leben der Blaualgen in Verbindung steht, hat bereits FERDINAND COHN seinerzeit erkannt. Diese Frage gehört zum Problem der Biolithogenese, das in der ersten Linie Geologen interessiert (PIA, PRÁT).

Des weiteren hat SCHWABE zuerst richtig erkannt, dass das Relief der Quelle, von dem auch die Wasserbewegung abhängt, für die Zusammensetzung der Besiedlung massgebend ist. Nach SCHWABES Vorschlag unterscheiden wir heute allgemein drei Typen von thermalen Biotopen: Rheikothermen mit rasch abfliessendem Wasser, Limnothermen mit kleinen Bassins, in denen sich das Wasser ansammelt und stagnierenden Charakter hat, und Helothermen in sumpfigem Terrain. Die verschiedenen morphologischen Biotope zeichnen sich auch durch verschiedene Biozönosen aus. So bevorzugen im allgemeinen Oszillatorien langsam und Phormidien rasch abfliessende Wässer.

Man hat zwar versucht die floristische Zusammensetzung dieser Biozönosen zu erfassen, doch ist es selbstverständlich, dass sich eine Lehre der thermalen Biozönosen erst nach der vollkommenen Erkennung der wichtigsten beeinflussenden Faktoren entwickeln kann. Das ökologische Studium der Thermalquellenbiologie befindet sich eben nach allem, was wir in grösster Kürze berichtet haben, erst im Stadium der Voruntersuchungen.

IV

In meinem am Anfang erwähnten Vortrag vom Jahre 1923 habe ich namentlich die Forderung nach einer eingehenden physiologischen Erforschung der Thermalorganismen aufgestellt. Die physiologische Erforschung einzelner

Organismen ist in gewisser Beziehung eine Vorbedingung für rein ökologische Forschung. Die physiologische Erforschung ist aber gänzlich ausgeblieben, was auch SCHWABE betont. Ganz isoliert stehen Untersuchungen, die ich selbst mit FR. Z. KLAS seinerzeit unternommen habe. Es handelte sich um physiologische Versuche mit der bekannten Thermalalge *Mastigocladus laminosus* (1939). Es konnte festgestellt werden, dass diese Alge in einer Nährlösung ohne Nitrate, d. h. ohne Stickstoff, als Anion gut gedeihen kann. Dieses Ergebnis ermutigt zu weiteren Untersuchungen, denn die Feststellung der Luftstickstoffbindung seitens der Thermalalgen wäre zweifellos für die allgemeine Biologie von besonderer Bedeutung. Woher *Mastigocladus* in diesem Falle die nötige Energie für die Assimilation des Luftstickstoffes hernimmt und inwieweit dabei eventuell die hohe Temperatur des Wassers im Spiele ist, bleibt vorläufig eine offene Frage.

Ausser Ernährungsproblemen der Thermalalgen wäre noch insbesondere ein zweites physiologisches Problem zu erwähnen. Dies ist das bereits öfters diskutierte Problem der *Resistenz der Thermalorganismen gegenüber hohen Temperaturen*. Dieses Problem befindet sich aber zur Zeit noch immer nur im Stadium theoretischer Besprechungen in Verbindung und Ablehnung an gewisse Hypothesen. Die Frage ist: was befähigt Blaualgen und auch Bakterien zur Ertragung solcher für das aktive Leben so hoher Temperaturen? Die allgemein bekannten Gesetze der Hitzekoagulation der Eiweissstoffe gelten im Bereiche der thermalen Blaualgen im allgemeinen nicht. Welche Substanzen die Ausfällung der Eiweissstoffe der Blaualgen hindern, wissen wir nicht. Auch der Einblick in die spezielle physiologische Literatur über die Hitzeresistenz gewisser Organismen (CAMERON, UVAROV, LARSEN, BĚLEHRADEK) kann uns darüber sehr wenig belehren. Es stehen uns eben zu wenig experimentelle Tatsachen zur Verfügung (BĚLEHRADEK) um an eine Lösung des Problems herantreten zu können. Die erste Aufgabe wäre hier, das Studium der Protoplasmatik der Blaualgen zu vertiefen. Vielleicht

handelt es sich doch, wie vermutet wird, um zwei verschiedene Plasmaarten, die der Akaryonten und die der Karyonten. Die Physiologie der Thermalalgen hat hier ein reiches Untersuchungsgebiet vor sich.

V

Nun kommen wir zur Besprechung des in der Literatur viel diskutierten Problems der Herkunft der Thermalorganismen, das in der Thermalbiologie unter dem Namen der „*Reliktenhypothese*“ bisher im Zentrum der thermalbiologischen Forschung stand. Diese, zuerst vom amerikanischen Geologen WEED aufgestellte und von den Botanikern WEST und DAVIS unterstützte Hypothese behauptete, dass Thermalalgen ihre Herkunft noch aus jenen geologischen Epochen der Erdentwicklung herleiten, in denen die Erdoberfläche mit heissen Gewässern überflutet war. Die Hypothese wurde einzig und allein auf die Tatsache des disjunkten Areales gewisser Blaualgen, wie *Mastigocladus* und *Phormidium laminosum*, gegründet. Diese disjunkten Mikroareale wären nach dieser Hypothese nur Relikte eines einstigen kontinuierlichen thermalen Areales. Die niedere Organisationsstufe dieser Algen gab dem historischen Gedanken eine weitere Stütze. Es blieb daher zu beantworten, ob diese Organismen in den Thermen autochthone Organismen darstellen oder doch als allochthone Elemente, d. h. aus dem gewöhnlichen Süßwasser in das heisse Mineralwasser eingewanderte Organismen aufzufassen sind. Dass es nicht leicht war, hier eine Entscheidung zu treffen, beweist die ausführliche wissenschaftliche Diskussion, die darüber geführt worden ist. ELENKIN, der namhafte russische Algologe, hat als erster seinerzeit diese Diskussion eröffnet, doch er konnte sich eigentlich weder für noch gegen die Hypothese entscheiden. Ich selbst beschäftigte mich mit dieser Hypothese in einem Vortrage am Internationalem Botanikerkongress 1926 in Ithaca und habe damals die Ansicht verteidigt, dass die thermalen Blaualgen nur an höhere Temperatur angepasste Organismen sind, also im Grunde allochthone Elemente im thermalen

Biotope sind, doch machte ich darauf aufmerksam, dass eine solche Einwanderung in verschiedenen Epochen der Erdentwicklung stattfinden konnte. Dafür sprach unter anderem auch die Tatsache der thermalen Vegetation einiger neuerschlossenen thermalen Quellen, wie der von Hájduóbbászlo in Ungarn (E. KOL) und der im Kaukasus, beschrieben von VORONICHIN. Die Besiedlung dieser Quellen bestand aus bekannten Blaualgen, die aus der Umgebung der Quellen eingewandert sind. Andererseits konnten wir feststellen, dass vadose (meteorische) Thermalquellen keine spezifische Thermalvegetation zeigen. Diesen Gedanken über biologische Unterschiede zwischen vadosen und juvenilen (magmatischen) Quellen hat später VORONICHIN auf Grund seiner Beobachtungen am Kaukasus aufgenommen und weiter ausgebaut. Trotz alledem gab es aber auch weiter entschiedene Vertreter der Reliktenhypothese. Der namhafte Biologe und Pflanzenphysiologe H. MOLISCH hat auf Grund seiner Beobachtungen in japanischen Thermen die Ansicht zu Gunsten der Reliktenhypothese vertreten. Er behauptete sogar, dass die ersten Pflanzen, die unseren Erdball besiedelten, wahrscheinlich thermophile, hohen Temperaturen angepasste *Cyanophyceen* und gewisse Bakterien waren, dieselben Organismen die noch heute Thermen bewohnen. Auch COPELAND, welcher die Thermalvegetation von Yellowstone untersuchte, hält es für wahrscheinlich, dass heutige Süßwasserblaualgen ihre Herkunft von Thermalarten ableiten. Was aber alle anderen in Thermen vorkommende Algengruppen ausser Blaualgen anlangt, so stimmen die meisten Autoren darin überein, dass sie in Thermen allochthone Elemente darstellen.

Nach ISSEL, und neuestens auch nach TUXEN, besteht auch die Thermalfauna durchwegs aus an das warme Wasser sekundär angepassten Tieren. Die Frage der Herkunft bleibt also nur für Blaualgen noch immer offen. Zur definitiven Entscheidung in der Reliktenhypothese kann uns nur die genauere Erforschung der Ökologie und insbesondere der Physiologie der Blaualgen führen.

VI

Wie wir schon anfangs angedeutet haben, ist in der neuesten Zeit die Erforschung der Biologie der Thermalquellen in Berührung mit der Medizin getreten. Der Mensch hat seit Urzeiten Thermalquellen vielfach auszunützen versucht: für Badezwecke, als Waschanlagen, in moderner Zeit auch für Heizungszwecke, vor allem aber für Heilzwecke. Wo immer eine Thermalquelle entdeckt worden ist, wurde sie vom Kulturmenschen zu einer Heilanstalt ausgebaut. So kamen diese Biotope auch in die Domäne der medizinischen Wissenschaften. In der neuesten Zeit entwickelte sich ein besonderer Wissenschaftszweig, die *Balneologie*, welche unter anderem als ihr Hauptproblem die rätselhafte Heilwirkung der thermomineralen Quellen zu lösen versucht. Die Balneologie bediente sich bisher hauptsächlich der Chemie als Hilfswissenschaft, in der Hoffnung, dass sie in den chemischen Bestandteilen des mineralen Wassers das wirksame Agens finden wird. Erst in der neuesten Zeit beginnt man einzusehen, dass auch biologische Eigenschaften der Thermalwässer zu deren heilkundlicher Charakteristik gehören (STOCKMEYER 1928). Es wurde auch die Ansicht ausgesprochen, dass man in den thermalen Biozöosen und ihren Gliedern Indikatoren für bestimmte heilkundlich wichtige Eigenschaften des thermalen Wassers suchen müsse (SCHWABE 1933, PRÁT 1934). Von der medizinischen Seite erkannte man zugleich, dass die eigentümliche Wirkung der thermomineralen Quellen auf den badenden Menschen, die allgemein als Balneoreaktion bekannt ist, an niederen und in erster Linie an einzelligen Organismen leichter zu erfassen wäre. Die französische balneologische Schule unter der Führung von BILLARD gab eine Reihe von wissenschaftlichen Arbeiten heraus, die sich mit dem Studium der biologischen Eigenschaften der thermalen Mineralwässer beschäftigten. Es zeigte sich, dass in dieser Beziehung Pflanzen als einfachere Organismen sehr geeignete Untersuchungsobjekte darstellen. Eine Reihe von Forschern (HARFUDER, STRANSKY, BRÜNNING,

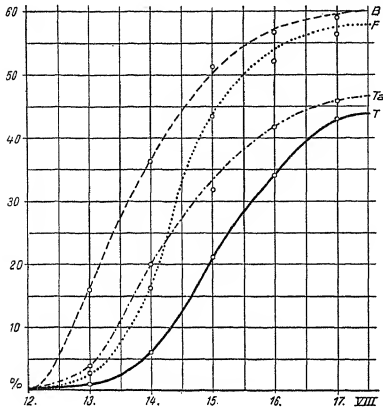


Abb. 5. Auskeimungsgeschwindigkeiten der Samen von *Fagopyrum esculentum* im Thermalwasser (T), Brunnenwasser (B), abgestandenem Thermalwasser (Ta) und im ferverisierten Wasser (F).

SCHILLER, BUKATSCH, JOSENNHANS, DYBOWSKI) benützten Pflanzenkeimlinge bzw. Keimungsprozesse zum Studium der Wirkung der thermomineralen Wasser. Dieses Studium ergab interessante und wichtige Resultate. Die thermomineralen Wasser der sog. Akrothermen zeigten die Eigenschaft der Verzögerung der Keimungsprozesse und Beschleunigung des Keimlingswachstums. Diese Wirkung liess sich nicht aus den bekannten Eigenschaften der thermomineralen Quellen herleiten, sie zeigte sich aber analog der Fervorwirkung (RADERMACHER und KLAS), d. h. der Wirkung des unter Druck von $2\frac{1}{2}$ Atm. auf 137°C erhitzten Wassers. Diese Analogie der Wirkung führte uns zum hypothetischen Schluss, dass die Wirkung des thermalen Wassers auf den Menschen auf natürlicher, im Erdinneren stattfindender Fervorisation des mineralen Wassers beruhe. Dieser neue Erklärungsversuch erschliesst neue Perspektiven zur Deutung des Geheimnisses der eigentlichen Heilwirkung. Unsere eigenen Versuche überzeugten uns, dass die keimungsverzögernde Wirkung des thermalen Wassers

nach dem Absteigen, d. h. nach der Alterung des Wassers, langsam abnimmt, ganz ähnlich wie es aus der Praxis bekannt ist, dass die Bäderwirkung nach Alterung des Thermalwassers ausbleibt. So steht vor uns das bekannte *Alterungsproblem* des thermomineralen Wassers. Das vorliegende Kurvendigramm (Abb. 5) eines unserer Versuche über die Wirkung des thermalen Wassers der Therme Krapina in Kroatien auf die Geschwindigkeit der Auskeimung der Samen von *Polygonum fagopyrum* zeigt uns die Unterschiede des frischen thermalen Wassers gegenüber abgestandenem thermalen Wasser, ferverisiertem Wasser und gewöhnlichem Brunnenwasser. Dieser Versuch beweist die bekannte Erscheinung der Alterung. Auf Grund dieser Vorversuche wollen wir an weitere Untersuchungen herangehen und versuchen, einen brauchbaren Phytotest für die Bewertung der Wirkung der Thermalwässer auszuarbeiten.

Aus diesen Versuchen und Überlegungen kommen wir zur Ansicht, dass die Geheimnisse der Heilwirkung nicht einfach im Chemosismus der Quelle bestehen, sondern vielmehr in den physikochemischen Eigenschaften (vielleicht Isotopenverschiedenheit), die sich nicht mit den bisherigen chemischen Analysen der Thermalwässer fassen lassen. SCHWABE spricht von der *Unausgeglichenheit (Instability) des thermomineralen Wassers*, das beim Erscheinen an der Oberfläche durch Druckveränderung und Entgasung seine Eigenschaften verändert. Es ist eine sehr wichtige Aufgabe der Physik und Physiologie, diese Eigenschaften des unausgeglichenen thermalen Wassers genau zu untersuchen. Wir glauben, dass eben hier der Schlüssel zur Klärung der geheimnisvollen Heilwirkung der Thermalwässer zu suchen ist. Die Verknüpfung der Biologie mit Balneologie wird auf diese Weise immer enger, so dass wir heute schon von einer *Balneobiologie* sprechen können, einer neuen wissenschaftlichen Disziplin, die sich mit den Beziehungen der Biologie zur Balneologie befassen soll.

Wir können hier nicht auf die gesamte balneobiologische Problematik eingehen. Es war nur unsere Aufgabe darauf hinzuweisen,

wie in der neuesten Zeit die Erforschung der Biologie der Thermen mannigfache neue Probleme aufgerollt hat und wie an deren Lösung in erster Reihe Botaniker mitgewirkt haben, was nur zur Ehre unserer „scientia amabilis“ dient.

Meine Damen und Herren!

Wenn wir am Schlusse unseres Vortrages noch einen Blick auf das zwar nur skizzenhafte Bild der biologischen Erforschung der Thermalquellen werfen, so müssen wir zunächst konstatieren, dass im letzten Vierteljahrhundert doch bedeutende Fortschritte erreicht worden sind, obwohl das wichtigste und das meiste noch lückenhaft geblieben ist. Wir haben gesehen, wie mannigfaltige neue ökologische, physiologische, historische, und auch medizinische Probleme dabei zum Vorschein kamen. Es zeigte sich, dass die Thermalbiotope nicht nur als „kuriose“ biologische Forschungsobjekte zu betrachten und werten sind, sondern auch wahrhafte Pretiosa der Wissenschaft darstellen, deren weitere wissenschaftliche Auswertung der Zukunft vorbehalten ist. Die anscheinenden Mikroprobleme dieser winzigen Inseln von warmem und heissem Wasser auf der Erdoberfläche mit ihrer eigenartigen Lebewelt verwandeln sich vor uns in

wahre Makroprobleme der gesamten allgemeinen Biologie, sowohl in der Theorie wie in der Praxis.

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EXHIBITS

In a laboratory room at the Department of Botany and Pharmacognosy of the Royal Pharmaceutical Institute botanical objects were exhibited. Dr. HEMMING VIRGIN was in charge of the exhibits and has reported the following contributions.

Prof. H. M. DIXON, Eire:

Experimental Demonstration of Sap-Tension in Plants: Photographic records of the movements of stems and petioles during transpiration may be used to demonstrate tension in their sap-supply. In these it was shown that fracture of the tensile stream arrests or reverses the movement. Photographic methods exhibited illustrated these results.

Prof. R. J. GAUTHERET, France:

Tissue cultures mounted on a board with description of the methods applied when making the cultures.

Dr. M. GODWARD, Great Britain:

Microscopic slides showing the cell division (with chromosomes) in *Spirogyra*.

Prof. TH. H. GOODSPEED, U. S. A.:

Elements of the California Flora; representative of several Life Zones and Plant Communities of the Pacific Coast of North America. These natural color photographs (enlargements of 35 mm Kodachrome) were exhibited through the courtesy of Mr. Brooking Tatum (681 Bayshore Blvd., Burlingame, California, U.S.A.) who during the past decade has portrayed in natural color most of the distinctive species of Pacific Coast floras and their ecological relations. From over 6000 Kodachromes his catalogue lists over 600 selected subjects,

which are available (both in 8" x 10" color prints and in 35 mm lantern slides) for herbaria and botanical instruction.

Mr. H. A. HYDE, Great Britain:

Photographs taken in the Asthma Research Department, Llandough Hospital, Cardiff. Fresh pollens are defatted with absolute alcohol and mounted in glycerin-gelatine-fuchsin. Magnification x 800. Photos paired. High focus: surface view. Median focus: optical section. Descriptive terminology provisional.

Mr. A. LIMA-DE-FARIA, Sweden:

Microscopic slides showing the cell division in *Secale* (pachyten).

Prof. H. MATSUURA, Japan:

Giant enlargement (photograph) of chromosomes of *Trillium*.

Mrs. LISELOTTE MOEWUS, Germany:

Photographs, herbarium specimens and microscopic slides showing the development of *Enteromorpha compressa* (in connection with a paper given in section TCR at the Congress).

Dr. DERK MULDER, Netherlands:

Various drawings and photographs showing phytopathological material.

Dr. JOHANNA C. SOBELS, Netherlands:

Cultures and photographs of myxomycetes.

Dr. S. SUNESSON, Sweden:

Chromosome slides.

Dr. J. H. TJO and Dr. ALBERT LEVAN, Sweden:

Microscopical slides of chromosomes showing the influence of oxy-quinoline on the cell division mechanism.

RECEPTIONS AND ENTERTAINMENTS

His Majesty the King had graciously invited the Congress members and their ladies to a reception at the Royal Palace of Drottningholm in the afternoon of the opening day, July 12th. On behalf of His Majesty the King the guests were received by the Crown Prince of Sweden, who shook hands with everyone of them. — During the excursion to Uppsala on July 16th arrangements had been made for a dinner with dance at the old Castle of Uppsala. — The Honorary presidents and the presidents were invited by the City of Stockholm to a luncheon in the Town Hall on July 18th. — In the evening of July 20th there was a farewell party in the Town Hall with Swedish folk-dances and modern dance.

Special entertainment programs were arranged for ladies not attending the meetings. On July 14th they could either visit the Gustafsberg potteries by invitation of the Cooperative Union and Wholesale Society or go on a sightseeing tour by boat "Under the Stockholm

Bridges", followed by a visit to Prince Eugen's Gallery at Valdemarsudde. On July 15th they were invited to the National History Museum and the Bergius Botanic Garden. Welfare institutions were demonstrated on July 17th, and a walk through the Old City with a visit to the Royal Palace was also arranged on that day.

On July 18th a tour to the old castle Skokloster with its famous collection of paintings and arms was arranged, and on July 19th there was a sightseeing tour to Sigtuna with a visit to the 11th century church of Ed, and to Antuna, a typical old Swedish mansion house. The owners of Antuna, Mr. and Mrs. CARL CURMAN, had invited the participants for tea. On July 18th and 19th the department store Nordiska Kompaniet was demonstrated and the participants in these demonstrations were invited for tea by the directors of the Company.

Many of the ladies also joined the general excursions on July 13th and 16th.

EXCURSIONS

In connection with the Congress two general excursions and 26 sectional excursions were arranged

GENERAL EXCURSIONS

I. On July 13th an excursion with 500 participants was arranged by boat to Utö. During the boat trip the general zonation of the vegetation in the archipelago was demonstrated by Professor L. G. ROMELL and Dr. E. ÅSPLUND. On Utö the flora was studied at various places.

II. On July 16th an excursion took place by special train from Stockholm to Uppsala,

where buses took approximately 1000 participants to the botanical institutions and botanical gardens of the University of Uppsala and of the Royal Agricultural College of Sweden. "Linnéträdgården" and "Linnés Hammarby", i.e. the Linnaeus Garden and the Linnaeus Estate at Hammarby, were also visited. The excursion ended with a dinner at the old Castle of Uppsala.

SECTIONAL EXCURSIONS

The sectional excursions took place before, during and after the Congress.

EXCURSIONS BEFORE THE CONGRESS

A I: Excursion in Skåne

Excursion A I of the Seventh International Botanical Congress which was arranged by the sections AGR, CYT, and GEN, started on July 6th with an informal reception at Akademiska Föreningen, Lund. The members of this excursion were divided into three groups, and each group made one bus tour on each of the three days July 7th, 8th and 10th. A special tour, also by bus, to eastern Skåne was arranged on Sunday, July 9th for those especially interested in fruit-tree breeding. This group visited the Balsgård Fruit Breeding Station at Fjälkestad. The other three tours for members of A I included visits to the following institutions:

Tour 1. Horticultural Research Station, Alnarp, Institute of Genetics and Botanical Garden, Lund. In the laboratory of the Genetics

Institute an exhibition of cytological slides had been arranged. Nineteen exhibitors showed slides of plant and animal material in 94 microscopes.

Tour 2. Svalöf Plant Breeding Institute (Swedish Seed Association) and the branch station at Svalöf of the Institute of Genetics, Lund.

Tour 3. Weibullsholm Plant Breeding Institute, Landskrona, Sugar Beet Breeding Institute, Hilleshög, Landskrona, and Institute of Forest Tree Breeding, Källstorp.

A special Ladies Program had been arranged with sightseeing in Lund and Malmö, an excursion to north-western Skåne, etc.

On Monday, July 10th, when all tours had been terminated, the members were invited by the Swedish Sugar Company to a dinner at Limhamn near Malmö. Other arrangements

during the excursion were supported by donations from plant breeding corporations, private persons, the town of Lund etc.

Leaders: The A I excursion was arranged by Prof. A. Müntzing in co-operation with Dr. A. Levan, Dr. I. Granhall, Dr. K. Fröier and Mrs. Z. Jakobsson. The heads of the institutes led the demonstrations in co-operation with their respective collaborators. (See further Excursion Guide A I.)

Participants: Prof. Sara Akdik, Turkey, Dr. J. T. do Amaral Gurgel, Brasil, Prof. R. Bamford, U.S.A., Dr. R. Bauer, Germany, Dr. I. Beckman, Brazil, Miss Margaret Blackwood, Australia, Prof. A. F. Blakeslee, U.S.A., Mr. J. Blencowe, Great Britain, Mr. A. Bradshaw, Great Britain, Miss Helena de Bruyn, Netherlands, Prof. F. Bustinza, Spain, Prof. A. Caballero, Spain, Ing. Agr. A. Chavancy, France, Dr. E. Cheesman, Great Britain, Dr. D. Clouston, Great Britain, Dr. C. D. Darlington, Great Britain, Mr. Teuan Davies, Great Britain, Mr. Wm. Ellis Davies, Great Britain, Prof. Th. Diannelidis, Greece, Dr. H. Douwes, North Sudan, Dr. F. Earnshaw, Great Britain, Miss Alice M. Evans, Great Britain, Mr. Gw. Evans, Great Britain, Miss Margaret Feigley, U.S.A., Dr. Naomi Feinbrunn, Israel, Dr. E. W. Fenton, Great Britain, Prof. Dr. J. Fitting, Germany, Mr. J. T. Flett, Great Britain, Mr. A. Foury, Morocco, Prof. R. Ruggles Gates, U.S.A., Prof. F. Galán, Spain, Ing. agr. H. R. Girginkoç, Turkey, Dr. Mary D. Glynn, Great Britain, Dr. Christine S. Gorter, Netherlands, Miss Barbara M. Gowdridge, Great Britain, Prof. F. Guinea, Spain, Dr. W. Hagborg, Canada, Doc. Cornelia Harte, Germany, Dr. Anna M. Hartsema, Netherlands, Mr. J. Hartshorne, Great Britain, Prof. A. Heilbronn, Turkey, Dr. Me-phara Heilbronn, Turkey, Dr. W. Hertsch, Germany, Miss Margaret Holden, Great Britain, Dr. N. Howard, Great Britain, Dr. R. Hull, Great Britain, Dr. E. C. Humphries, Great Britain, Prof. Cl. Jacquot, France, Dr. Edna L. Johnson, U.S.A., Prof. Le Roy P. V. Johnson, Canada, Mr. Paul Axel Johnson, U.S.A., Dr. Margaret A. Keay, Great Britain, Dr. D. D.

Keck, U.S.A., Dr. Louise Kerling, Netherlands, Mag. Sc. A. Kjaer, Denmark, Mrs H. Kjaer, Denmark, Prof. E. Knapp, Germany, Dr. R. L. Knight, North Sudan, Mrs. A. M. Koster-Bouman, Netherlands, Mr. D. M. Koster-Bouman, Netherlands, Dr. Ir. Kusnoto, Indonesia, Mr. L. Larter, Great Britain, Dr. J. W. Lesley, U.S.A., Dr. Margaret Lesley, U.S.A., Dr. A. Levan, Sweden, Dr. L. Ling, China, Miss Thoraya Lotfy, Egypt, Miss Evadne Fenn Lusher, Great Britain, Prof. G. A. L. Mehlquist, U.S.A., Dr. P. Michaelis, Germany, Doz. Dr. Franz Moewus, Germany, Dr. Liselotte Moewus, Germany, Mag. K. Multamäki, Finland, Prof. Dr. K. O. Müller, Germany, Dr. Mina Nadel-Schiffman, Israel, Prof. Lillian Nagel, U.S.A., Mr. R. Neve, Great Britain, Prof. A. J. P. Oort, Netherlands, Prof. H. Oppenheimer, Israel, Mrs. H. Oppenheimer, Israel, Mr. M. Panjan, Yugoslavia, Dr. Elena Paunero, Spain, Dr. Elizabeth Peabody, U.S.A., Fil. lic. Ann-Margret Perje, Sweden, Prof. B. Peroynel, Italy, Prof. M. Plaut, Israel, Mrs. Alice Plaut, Israel, Dr. J. M. Poehlman, U.S.A., Mrs. Rose Poehlman, U. S. A., Prof. A. Quintanilha, Portugal, Prof. L. F. Randolph, U.S.A., Dr. W. Rasch, Sweden, Mrs. W. Rasch, Sweden, Prof. R. Rol, France, Dr. H. Ross, Germany, Mr. T. Ruden, Norway, Prof. Dr. W. Rudolf, Germany, Mrs. Margot Rudolf-Lauritsen, Germany, Miss J. C. Schreuder, Netherlands, Graf A. F. von der Schulenburg, Germany, Gräfin Elisabeth von der Schulenburg, Germany, Dr. N. Simmonds, Trinidad, B. W. I., Dr. Johanna Sobels, Netherlands, Dr. Mildred Southwick, U.S.A., Miss Dina Spierenburg, Netherlands, Prof. N. Sylvén, Sweden, Prof. M. C. Tariman, Turkey, Mr. A. S. Thomas, Great Britain, Mr. K. F. Thompson, Great Britain, Miss Joan Thurston, Great Britain, Dr. M. Urries, Spain, Dr. J. Venkateswarlu, India, Mr. R. K. Vickery, U.S.A., Dr. Donald J. Watson, Great Britain, Dr. Marion A. Watson, Great Britain, Dr. G. Watt, Great Britain, Prof. F. W. Went, U.S.A., Dr. Johanna C. Went, Netherlands, Mr. John H. Wilson, Great Britain, Doc. E. Åkerberg, Sweden.

ARNE MÜNTZING

A II a 1: Phytogeographical Excursions in Eastern Skåne

The excursion started in Lund on June 27th. The first day was devoted to studies of the vegetation in the calcareous fens at Benestad, on the sandy fields east of Ystad (the fields of Nybro) and on the sea shores at Sandhammaren. The participants stayed over night in Simrishamn and continued on June 28th to Stenshuvud, where the undergrowth in the hazel and hornbeam forests as well as the rock vegetation were studied. The rest of the day was spent at Vittemölla, where the zonation of the vegetation was studied.

After a short visit to the old castle of Glimmingehus in the morning of June 29th, the party proceeded to Tjörnedala, famous for the detailed vegetation analyses and descriptions made by LINNÆUS on his Scanian Journey in 1749. The next stop was Andrarum, where the undergrowth in the deciduous forest at Breabäck was studied. Also the vegetation on different types of grasslands in the valley of the stream Verkeån was analysed.

On June 30th the tour continued to Ålahäcken in Trolle-Ljungby via Degeberga and Everöd. In the afternoon calcareous fens and the sea shore vegetation were studied at Ålahäcken. From Sölvesborg, the excursion continued on July 1st to Åhus in order to examine the vegetation on sea shores and sandy grasslands and in planted coniferous woods. The tour then went north to the moraine area. The shore vegetation around the lake Immeln was studied and among other plants *Lycopodium inundatum*, *Rhynchospora fusca*, *Lobelia* and *Littorella* were found. The next stop was Nyteboda pine wood reservation, where a woodland pool with a shore vegetation of *Ledum*, *Andromeda*, *Carex limosa* and *Carex pauciflora* was studied. On the way back to Sölvesborg stops were made at Vånga and Bäckaskog, where the shore vegetation at the lake of Oppmanna was analysed. Among others *Senecio palustris* and *Stellaria aquatica* were found. The excursion ended at Sölvesborg in the evening of July 1st. (See further Excursion Guide A II a 1.)

Leaders: Professor H. Weimarck and Docent T. Norlindh.

Participants: Prof. Arthur Clapham, Great Britain, Miss Ann Conolly, Great Britain, Miss Elizabeth Davies, Great Britain, Prof. Knut Faegri, Norway, Miss Denise Neugnot, France, Miss Bess Reed Peacock, U.S.A., Prof. Thomas Gaskell Tutin, Great Britain, Prof. Dr. Reinhold Tüxen, Germany.

H. WEIMARCK and T. NORLINDH

A II a 2 (Blekinge): Phytogeographical Excursion through Blekinge

This one-day excursion which started in Sölvesborg took place on July 2nd.

A short stop was made in the "meadow beech forest" (field layer, i.e., *Asperula odorata*, *Convallaria majalis*, *Stellaria Holostea*) at Valje to the west of Sölvesborg. At Norje, 10 km northwest of Sölvesborg, one hour was devoted to the study of the sea shore vegetation (i.e., *Cakile maritima*, *Centaurium glomeratum*, *vulgare* and *pulchellum*, *Hydrocotyle vulgaris*, *Lotus corniculatus*, *Plantago Coronopus* and *maritima*, *Potentilla anserina*, *Scirpus planifolius*, *rufus*, *Tabernaemontani* and *uniguinis*, *Trifolium fragiferum*, *Triglochin maritimum* and *palustre*). At Tubbaryd immediately west of Karlshamn a stop was made at a small deciduous forest (*Fagus*, *Quercus*, *Tilia*, *Carpinus*) which has a rich vegetation of herbs, i.e., *Dentaria bulbifera*, *Festuca alliissima*, *Lathyrus niger*, *Melica nutans* and *uniflora*, *Sanicula europaea*, *Stellaria nemorum*.

Count H. WACHTMEISTER, who had joined the excursion, invited the participants to luncheon at the Skärva mansion house near Karlskrona.

A very fine growth of *Osmunda regalis* was noted at Nättraby in the river Nättrabyån. The latter part of the afternoon was devoted to the study of the vegetation in the lakes of north-eastern Blekinge. Short stops were made at the eutrophic lake Niklastorpgölen (*Cladium Mariscus*, *Lotus uliginosus*) and the oligotrophic lakes Sännen (*Lycopodium inundatum*, *Myrica Gale*) and Hörnen (*Lobelia Dortmanna*). At Fur

near the Småland boundary *Thesium alpinum* was observed. The excursion ended at Kalmar in the evening. (See further Excursion Guide A II a 2, Blekinge.)

Leader: Dr. O. Almborn.

Participants: Mr. A. Alston, Great Britain, Dr. Henriette Bartoo, U.S.A., Mr. P. Bell, Great Britain, Dr. Kathleen Blackburn, Great Britain, Dr. B. Boivin, Canada, Mrs. Cosette Boivin, Canada, Dr. T. Böcher, Denmark, Prof. A. Clapham, Great Britain, Dr. W. Clark, Great Britain, Miss Ann Conolly, Great Britain, Miss Elizabeth Davies, Great Britain, Prof. K. Faegri, Norway, Dr. F. Fosberg, U. S. A., Prof. Dr. H. Gams, Austria, Miss Mary Gibby, Great Britain, Mrs. Nellie Gibby, Great Britain, Miss Britta Mannerfelt, Sweden, Dr. F. Mattick, Germany, Miss Denise Neugnot, France, Miss Bess Reed Peacock, U. S. A., Prof. T. Tutin, Great Britain, Prof. Dr. R. Tüxen, Germany, Prof. D. Webb, Eire.

O. ALMBORN

A II a 2 (Öland): Phytogeographical Excursion on the Baltic Island of Öland

The participants gathered at Kalmar in the evening of July 2nd, where they were accommodated during the excursion. Every morning they had to cross the Kalmar Sund.

The aim of the tour on July 3rd was to study the vegetation of the *Large Alvar* of Southern Öland. "Alvar" is a popular local term for the flat, almost treeless landscape found on the bare or thinly soil-covered limestone bed. The Large Alvar extends about 40 km in the direction north-south and maximum 10 km east-west. In central and northern Öland there are many smaller Alvars. During the day a stroll of about 15 km was made in the central part of the Large Alvar from the village of Vickelby in the general direction east to southeast to the lake Möckelmossen, where the participants became acquainted with many plants and plant communities, representative of the peculiar flora and vegetation of the Alvar, as well as with the most important ecological factors. During a short excursion on the following day in the northern-

most part of the Large Alvar special attention was given to the changes of the vegetation in the transition zone between a comparatively natural birch wood on a rather shallow, calcareous ground-moraine and the Alvar. The extensive, low brushes of *Potentilla fruticosa* were studied.

July 5th was devoted to a bus trip around the central part of the island. The main object of this trip was the study of some rich deciduous woods and a *Sarmatian sand grass heath*. On July 6th the participants were free to spend the day according to their own will. As it was raining, most of them remained at Kalmar. (See further Excursion Guide A II a 2, Öland.)

Leaders: Dr. Rikard Sterner and Dr. Nils Albertson.

Participants: Mrs. E. Albertson, Sweden, Dr. O. Almborn, Sweden, Mr. Arthur Alston, Great Britain, Dr. Henriette V. Bartoo, U. S. A., Mr. Peter Bell, Great Britain, Dr. Kathleen Blackburn, Great Britain, Dr. Bernhard Boivin, Canada, Mrs. Cosette Boivin, Canada, Dr. Tyge Böcher, Denmark, Prof. Arthur Clapham, Great Britain, Dr. William Clark, Great Britain, Miss Ann Conolly, Great Britain, Miss Elizabeth Davies, Great Britain, Prof. Dr. Knut Faegri, Norway, Dr. F. Fosberg, U. S. A., Prof. Dr. Helmut Gams, Austria, Mrs. A. Nellie Gibby, Great Britain, Miss Mary Gibby, Great Britain, Prof. Dr. Aarno Kalela, Finland, Prof. Mauno J. Kotilainen, Finland, Cand. Hort. Britta Mannerfelt, Sweden, Dr. Fritz Mattick, Germany, Miss Denise Neugnot, France, Mr. Max v. Osten, Netherlands, Miss Bess Reed Peacock, U. S. A., Prof. Thomas G. Tutin, Great Britain, Prof. Dr. Reinhold Tüxen, Germany, Prof. David Webb, Eire.

RIKARD STERNER

A II a 3: Phytogeographical Excursions in Gotland

The excursion aimed at giving the most complete picture possible of the flora and vegetation of the island of Gotland. Special attention was devoted to the connection between the geographical foundation and the vegetation and

also to continuous changes in the vegetation caused by the influence of man and by fluctuations in climate.

During the excursion, which lasted from July 7th to 10th, different types of flat limestone grounds and their vegetation were demonstrated. In the same areas the vegetation on loose soil layers, deficient of lime, was also studied. On the open limestone grounds the northern and southern species found in the vegetation were given special attention; the phanerogames as well as the mosses and lichens were studied. The most evident changes in the vegetation, such as the heavy thinning in the stands of *Pinus* and *Juniperus* or in the mats of *Arctostaphylos* and *Calluna*, were demonstrated, and the typical invasion of deciduous trees and shrubs was pointed out. Comparisons were made between heavily grazed areas of today and areas where the grazing had been stopped or reduced.

The topography and hydrography of the mires were studied. The vegetation in the flat fens and the more or less sloping spring fens was particularly noticed. The many northern and southern species in the vegetation were demonstrated. Species of *Carex* and *Orchis* were studied and a new form of *Orchis*, which is intermediate between *Orchis incarnata* and *Orchis Traunsteineri*, was given special attention. A mire complex in Västkinde, north of Visby, aroused special interest, since *Ranunculus ophioglossifolius* (only in Gotland in northern Europe) was found in a little pool dried up in summer, where its occurrence is evidently conditioned by grazing and trampling of horses.

The consequences of the extreme artificial drainage in the island during the last century were studied and discussed at many places.

The sea shore vegetation was studied at several places along the coast line and so were such changes in the composition of the shore vegetation as the rapid increase of *Elymus*, *Ammodendron* and *Lactuca tatarica*.

In the coniferous woods, which are no longer grazed, the rapid invasion of deciduous trees and shrubs, especially species of *Sorbus*, was

shown. This change is typical, above all, along the coasts. (See further Excursion Guide A II a 3.)

Leader: Mr. Bengt Pettersson.

Assistant leaders: Mrs. Anna-Greta Pettersson, Mr. Lars Dahlgren and Mr. Sten Forselius.

Participants: Dr. A. A. Aleem, Egypt, Dr. Henriette V. Bartoo, U. S. A., Mr. Peter R. Bell, Great Britain, Dr. Kathleen Blackburn, Great Britain, Dr. T. W. Böcher, Denmark, Mrs. Kirsten Böcher, Denmark, Prof. A. R. Clapham, Great Britain, Dr. W. Clark, Great Britain, Miss Elizabeth Davies, Great Britain, Mr. R. El Halwagy, Egypt, Prof. K. Faegri, Norway, Prof. H. Gams, Austria, Mrs. Nellie A. Gibby, Great Britain, Miss Mary Gibby, Great Britain, Ing. agr. A. G. Haudricout, France, Mr. O. Hotchkiss, U. S. A., Dr. J. Iversen, Denmark, Dr. J. Jalas, Finland, Prof. A. Kalela, Finland, Prof. M. J. Kotilainen, Finland, Mr. O. Lehtonen, Finland, Mr. J. Lounamaa, Finland, Cand. hort. Britta Mannerfelt, Sweden, Dr. F. Matlack, Germany, Dr. Alberta Mennega, Netherlands, Miss Denise Neugnot, France, Doc. Hedda Nordenskiöld, Sweden, Mr. M. v. Oosten, Netherlands, Dr. Bror Pettersson, Finland, Mrs. Årla Pettersson, Finland, Prof. N. Söyrinki, Finland, Miss Mary A. Todd, Australia, Prof. T. G. Tutin, Great Britain, Prof. D. Webb, Eire.

BENGT PETTERSSON

A II b: *Phytogeographical Mire Excursions*

1. The Billingen-Falbygden district in Västergötland (south-western Sweden), July 1st-5th.

2 (first part). The raised bog Komosse, July 6th-7th.

2 (second part). North-eastern Småland and Östergötland, July 8th-9th.

3. The Ryggmossen mire near Uppsala, July 10th.

Chief aim of the excursion: Studies of the major types of living mire vegetation, and of the correlation between mire vegetation and mire water.

1. *Bog (Hochmoor, haute tourbière).* Raised

above the mineral ground water level, nourished only by rain and snow. Water very acid, very poor in electrolytes. Vegetation very poor in species (of *Carex* only *C. limosa*), consisting of alternating *Sphagnum* hummocks with much *Calluna* and hollows with wet *Sphagnum* carpets and much *Eriophorum vaginatum*. The south-western or Komosse type of bog (studied on Mt Billingen and on the Komosse bogs) is characterized by the presence of oceanic species (e.g. *Erica tetralix*) lacking in the other bog types, and of species restricted to fen in the more continental parts (e.g. *Sphagnum imbricatum* and *papillosum*), as well as by the predominance of red *Sphagnum* (*S. magellanicum* and *rubellum*) in the hummock and upper hollow vegetation. In the north-eastern or Ryggmosse type of bog, the red *Sphagna* are entirely replaced in the hummocks by the brown *S. fuscum* and in the upper hollow stage by *S. balticum*. In the intermediate Skagershultsmosse type (studied on the bog Breafallsmossen in NE Småland) *S. fuscum* occupies only the upper hummock stage; in the Komosse type, it is restricted to small secondary hummocks sometimes following the *Cladina* stage. In the lower hollow stage of all bog types *Sphagnum cuspidatum* is predominant. — The open bog plane is always surrounded by a drier marginal bog slope, with low *Pinus silvestris* forest (least developed on some Komosse bogs), much *Vaccinium uliginosum*, *Ledum palustre* except in the South-West, and much *Sphagnum parvifolium* (very rare on the bog plane).

II. *Fen* (*Flachmoor, basse tourbière*). A bog is, more or less continuously, surrounded by a fen zone or a lagg, in which drainage water from the bog is mixed with mineral ground water. The border between bog and fen, the mineral ground water limit, is often sharp, marked by the sudden appearance of a remarkable number of exclusive fen plants (*Carex rostrata*, *lasiocarpa*, and *pauciflora*, *Eriophorum angustifolium*, *Sphagnum apiculatum*, *Pinnularia* spp., etc.). *Fen soaks* (Rüllen) often lead mineral water from springs, or mineral ground islands, in a bog down into the lagg. *Fen windows* in the bog

are caused by a slight outflow of mineral ground water. Besides the mires formed by both bog and fen, there are mires formed by fen only. Most of the fen bordering bogs and of the fen in non-calcareous districts is *poor fen* (Armflachmoor, basse tourbière pauvre, *Apiculation* alliance), poor in species (though not as poor as the bog), with a bottom layer chiefly formed by *Sphagna*, partly the bog species mentioned above, partly exclusive poor fen species (among which *S. apiculatum* and *Dusenii* are frequent dominants). The poor fen water is acid (but usually less acid than bog water) and poor in electrolytes (though richer than bog water). In the calcareous Falbygden district the participants in the excursion saw various types of *rich fen* (Reichflachmoor, basse tourbière riche, *Scorpidion* alliance), rich in species, with a bottom layer formed by *Scorpidium scorpioides*, *Drepanocladus intermedius*, *Campylopus stellatus* and other "brown mosses" together with a few of the most demanding *Sphagnum* species, e.g. *S. warnstorffianum*. The rich fen water is circumneutral, rich in electrolytes and especially rich in Ca. The most extreme rich fen is characterized by *Schoenus ferrugineus*, *Carex lepidocarpa* and other extreme calciphytes. (See further Excursion Guides A II b 1, A II b 2 (first part), A II b 2 (second part) and A II b 3.)

Leaders: Prof. G. Einar Du Rietz and Miss Margareta Witting (1, 2, 3), and Prof. Hugo Osvald (2).

Assistant leaders: Mr. Lennart Fridén (1), Dr. Magnus Fries (1), Mr. Nils Stålberg (1, 2).

Participants: Prof. Faridoon Bharucha, India (1), Prof. William Brown, Great Britain (2, 3), Mrs. Marguerite Bulman, Great Britain (1, 2, 3), Miss Ann Conolly, Great Britain, (2, 3), Dr. Verona Conway, Great Britain (1, 2, 3), Dr. Evelyn Fernald, U. S. A. (1, 2, 3), Dr. Olav Gjaerevoll, Norway (2, 3), Mr. Erik Hellgren, Sweden (1), Dr. Robert Kolbe, Sweden (3), Dr. Werner Lüdi, Switzerland (1, 2, 3), Mr. Wim. Meijer, Netherlands (2), Mr. G. F. Mitchell, Eire (2), Dr. Tage Nilsson, Sweden (1, 2), Prof. William Pearsall, Great Britain, (1, 2, 3), Prof. Robert Potonié, Germany (2), Miss Siri von

Reis, U. S. A. (1, 2, 3), Dr. A. J. Rutter, Great Britain (2, 3), Mr. Herbert Straka, Germany (1, 2), Mr. Jaan Terasmäe, Sweden (1), Mr. Kuno Thomasson, Sweden (1, 2, 3), Prof. Roelof van der Wijk, Netherlands (1, 3).

G. EINAR DU RIETZ

A II c: Salt Marsh Excursion on the West Coast of Sweden

The chief aim of the excursion was to give an idea of the vegetation of the Swedish West Coast with special emphasis on the sea shores and salt marshes. The excursion took place from July 6th to 10th. During the first day the Botanical Garden of Gothenburg and Bondegården in Jonsäter (Ing. E. MAGNUS) were visited.

On July 7th the party proceeded to Stora and Lilla Amundön, about 15 km south of Gothenburg, were salt marshes of different types, rocky and sandy shores and the vegetation in the deciduous forest region, were studied. This region is almost untouched by human hands and no coniferous woods are found. On the sea shore a number of northern species were found, such as *Haloscias scoticum*, *Carex maritima*, *Carex paleacea*, *Carex recta* and *Angelica Archangelica* ssp. *litoralis* and also some western species as *Aira praecox*, *Erica tetralix*, *Lonicera Periclymenum*, *Pedicularis silvatica*, *Sagina subulata*, *Teesdalia nudicaulis* and *Sedum anglicum*. On southern slopes *Quercus petraea* was found, and on northern *Populus tremula*.

The whole day of July 8th was devoted to the Onsala peninsula. The salt marsh in the inner part of Kungsbackafjärden was demonstrated. *Scirpus parvulus*, *Carex paleacea* and *C. recta* are found here in abundance and the rare and for Halland new species, *Carex Mackenziei* also occurs. In an oligotrophic lake *Lobelia Dortmanna* was found flowering and *Pilularia globulifera* appeared. In a pool *Echinodorus ranunculoides*, *Apium inundatum*, *Littorella uniflora* were found growing and on the rocky shores at Råö *Crambe maritima* occurred in abundance. At Särö *Quercus petraea*, a spon-

aneous coniferous wood, and an imposing stand of yew were shown.

On July 9th the excursion continued across the island of Orust over to the island of Tjörn. Oak woods at Sundsby, calcareous soils with *Cirsium acaule* and other species requiring lime were studied. *Alchemilla alpina* was demonstrated as a remnant of the arctic flora. On the rocky shores *Mertensia maritima* and *Glaucium flavum* were growing. The German botanists were especially interested in the "Trockenrasengesellschaften" with *Spergula vernalis*, *Aira praecox* and *Teesdalia nudicaulis*, which are highly characteristic of rocky areas in Bohuslän.

The last day of the excursion was spent at Vrångö in the southern Gothenburg Archipelago. The boat trip from Gothenburg to Vrångö gave a good impression of what the archipelago in Western Sweden is like. The observations of the vegetation on the island of Vrångö only confirmed those made during the former part of the excursion. (See further Excursion Guide A II c.)

Leader: Mr. Vilhelm Gillner.

Assistant leader: Mr. Reinhold Ivarsson.

Participants: Prof. F. Bharucha, India, Dr. Clair Brown, U. S. A., Miss Ulla Bärlund, Finland, Docent Carl Cedercreutz, Finland, Prof. V. J. Chapman, New Zealand, Prof. E. Häyrén, Finland, Mrs. Ann-Marie Häyrén-Malmström, Finland, Mr. Matti Kaasinen, Finland, Mr. Lalli Laine, Finland, Mrs. Brita Schwank, Finland, Prof. O. Stocker, Germany, Prof. R. Tüxen, Germany, Dr. H. Vallin, Sweden, Prof. H. Walter, Germany.

VILHELM GILLNER

A II d: Phytogeographical Forest Excursion in South Sweden

The excursion took place from July 5th to 10th. Its aim was to demonstrate the forest vegetation as influenced by Man and to compare it with the forest vegetation in typical old stands in south-western Sweden. First the forest free plains in South Skåne were visited, and the salt marshes and the heaths round Skanör were

studied. In Dalby Söderskog the participants were shown a mixed deciduous forest with ancient character growing on the lime-rich soils in south-western Skåne. In this connection the strong influence of civilization on the composition of the forest vegetation was discussed, which has during the centuries become more and more intensive.

After a visit to Ramlösa Plantskola (the Tree Nursery at Ramlösa) for studies of modern forest tree breeding, the vegetation on the sandstone and iron-gneiss moraines in the central parts of Skåne, especially the beech forests, was studied for one and a half day. The southern beech forest region ends at Kristianstad, where the southern limit for the spruce forests is passed. Mrs. Weimarck here demonstrated how forest fires and primitive farming on those lands had influenced today's vegetation in the South-Swedish coniferous forests. On the way from Nyteboda to Tromtö the competition between spruce and beech in southern Blekinge was studied. The tour continued to Karlskrona and then went north through the beech-spruce area in Småland. The northern limit of this area was passed at Vrigstad.

Some of the outpost areas of beech were visited on the way to Jönköping, where the South-Swedish pine bog areas were studied. The excursion ended at Omberg, where the rich virgin forest of spruce and beech on the steep slopes as well as old plantations of different conifers were demonstrated. (See further Excursion Guide A II d.)

Leader: Prof. Bertil Lindquist.

Assistant leaders: Dr. N. Dahlbeck, Mr. Tors-ten Håkansson and Mrs. Gunhild Weimarck.

Participants: Mrs. Gienna Arsenau, U. S. A., Mr. R. W. Becking, Netherlands, Mrs. Jean Daubenmire, U. S. A., Dr. R. F. Daubenmire, U. S. A., Prof. R. O. Earl, Canada, Miss Mildred E. Faust, U. S. A., Prof. Hans H. H. Heiberg, Norway, Mr. H. Jensen, Sweden, Mr. A. W. Jessep, Australia, Mrs. Dorothy Jessep, Australia, Mr. M. Ksiez, Denmark, Miss Margaret Mc Kibbin, Canada, Prof. G. Negri, Italy, Miss Bess Reed Peacock, U. S. A., Dr. E. W. J. Phil-

ips, Great Britain, Dr. S. Selander, Sweden, Dr. W. von Wettstein, Austria.

BERTIL LINDQUIST

A III a: Algological Excursion to the Swedish West Coast

The main intention of the excursion was to give the participants an idea of the algal flora of the Swedish West Coast. It can be looked upon as a more or less reduced flora of north-western Europe. Decreased salinity — 20–30 ‰ in the surface water — is generally considered to be responsible for the reduced number of species and, in several cases, also for the small size of the plants. The tide is practically lacking at the Swedish West Coast, but there are occasional changes of the water level up to 0.5 m due to winds, currents and so on. It is therefore most interesting to compare the vegetation on this littoral zone in Sweden with that in Western Europe.

The excursion started on July 5th in Gothenburg on board the research ship "m/s Skagerak" along the coast to the Kristineberg Marine Station at Fiskebäckskil, where lodging was arranged. Every day excursions were made by boat to different localities and the collected material was studied in the afternoon.

The first day was spent on Bonden, an extremely exposed island, with good possibilities for studies of the composition of the vegetation of an exposed littoral zone with *Chaetomorpha aerea*, *Spongomorpha pallida*, *Pylaiella rupicola*, *Bangia fuscopurpurea*, *Ceramium penicillatum* and *secundatum*, *Corallina officinalis*, *Polysiphonia Brodiaei* and so on.

The next day was spent dredging at Smedjan, an exposed locality with occurrence of *Laminaria Cloustonii* and a great number of deep water Rhodophyceae as *Antithamnion plumula*, *Bonne-maisonia asparagoides*, *Callithamnion*, *Ceramium* and *Polysiphonia* species etc., further at Flatholmen and Mosseberget, two somewhat sheltered localities where *Laminaria digitata* and *saccharina*, *Halidrys* and various Phaeophyceae and Rhodophyceae occur.

July 8th a tour was arranged to Strömmarna, a peculiar, sheltered locality with very strong current. Among other species *Fucus serratus*, *Laminaria saccharina*, *Lithothamnion* spp., and *Griffithsia corallina* were found. The afternoon was used for shore collection at Blåbärsholmen, where the vegetation on sheltered shore with well developed belts of fucoids as well as an exposed shore with numerous filamentous Phaeophyceae and Rhodophyceae could be studied.

On the last day a long trip was undertaken to Hällö and Smögen. Dredging was made at some places. It may be specially mentioned that *Chylocardia kaliformis* and *Dictyota dichotoma* were found, as these two species occur but rarely in Sweden. (See further Excursion Guide A III a.)

Leader: Dr. Tore Levring.

Participants: Miss Dorothy Bexon, Great Britain, Dr. Helen Blackler, Great Britain, Dr. Carl Bliding, Sweden, Prof. Hugo L. Blomquist, U. S. A., Prof. Trygve Braarud, Norway, Mr. Tyge Christensen, Denmark, Dr. Elsie Conway, Great Britain, Dr. E. Yale Dawson, U. S. A., Mrs. Maxine Dawson, U. S. A., Miss Carola Dickinson, Great Britain, Dr. Kathleen Drew Baker, Great Britain, Prof. Jean Feldmann, France, Mr. Edward Holsinger, Ceylon, Mr. Erik Jaasund, Sweden, Prof. J. Harlan Johnson, U. S. A., Mrs. Elsa Kylin, Sweden, Mrs. Elsa Levring, Sweden, Dr. Alf Lindstedt, Sweden, Mr. Søren Lund, Denmark, Mr. Hans Luther, Finland, Dr. Margaret Martin, Great Britain, Miss Lucy B. Moore, New Zealand, Dr. Betty Moss, Great Britain, Dr. Mary Parke, Great Britain, Miss Hilda Parkes, Eire, Mr. Bengt Peters, Sweden, Mrs. Daisy Pollard, Great Britain, Mr. Henry Th. Powell, Great Britain, Mr. A. Schotter, Algérie, Mr. E. Schotter, Algérie, Mr. G. P. Schotter, Algérie, Prof. Gilbert M. Smith, U. S. A., Mrs. Helen Smith, U. S. A., Dr. Svante Suneson, Sweden, Prof. William Taylor, U. S. A., Mr. F. T. Walker, Great Britain, Mr. Tore Wennberg, Sweden, Dr. F. N. Woodward, Great Britain, Prof. Walter Zimmermann, Germany.

TORE LEVRING

A III b: Lichenological Excursion to the Island of Skaftö in Bohuslän

This excursion aimed especially at demonstrating West Swedish marine and maritime lichens and lichen societies as well as their dependence on different milieu conditions.

The excursion lasted for five days, and the weather was fine all the time. In the morning of July 6th most participants took a steamer from Gothenburg to the town of Lysekil, which was the headquarters. In the evening a tour went to Stångehuvud for studies of the zonation of the marine lichens on a very exposed part of the coast. — On July 7th there was an excursion to the small islets of Rödsåren and Högaråren outside the biological station Klubban, for demonstration of marine lichens and lichen societies. — On July 8th there was an excursion to Vägeröd. — One excursion was made by train on July 9th to Brodalen in the mainland west of the Gullmar fjord to study the lichen flora and vegetation in an inland district, and another by boat on July 10th to the east side of N. Skaftö (Skaftö, Lunnevik) and to the parish of Dragsmark in the mainland opposite Skaftö, in order to demonstrate some rare oceanic lichens (*Cetraria norvegica*, *Sticta silvatica*). In the morning of July 11th most participants left by train for Stockholm.

During these excursions some interesting observations and finds were made. — In the book written by the present author in 1939, 433 different lichen species are mentioned. Another six are, however, to be added as detected later on in my old or newer collections (*Lecidea turgidula*, *Cladonia caespiticia*, *Pertusaria leprarioides*, *Parmelia tinctoria*, *Rinodina pyrina*, *Lepraria glauccella*). — During this last excursion to Skaftö another five species were found, viz. *Calicium abietinum* (L. Skaftö, SANTESSON), *Opegrapha viridis* (Vägeröd, ALMBORN), *Lecidea silacea* (Östersidan, DEGELIUS), *Lecanora intrudens* (Östersidan, MAGNUSSON), *Lecania Ralskii* (Rödsåren, MAGNUSSON). The total number of lichen species at N. Skaftö is thus 444 so far. Outside Skaftö were recorded

i.a. *Coniocypopsis arenaria* (Dragsmark: Berg, EILIF DAHL) and *Parmelia revoluta* (Bro: Broberg, ALMBORN), both new for Bohuslän (like *Opegrapha viridis*).

The guide book used during the excursion was: DEGELIUS, G., Die Flechten von Norra Skåftön (Uppsala Univ. Årsskr. 1939:11, Uppsala 1939).

Leader: Dr. Gunnar Degelius.

Participants: Dr. O. Almborn, Sweden, Mr. Eilif Dahl, Norway, Mr. Per-Olof Lindahl, Sweden, Dr. R. A. Maas Geesteranus, Netherlands, Dr. A. H. Magnusson, Sweden, Prof. T. S. Sadasivan, India, Mr. R. Santesson, Sweden, Dr. C. V. Subrahmanyam, India.

GUNNAR DEGELIUS

EXCURSIONS DURING THE CONGRESS

B1: Phytogeographical Excursion to the Maritime Birch Forest Zone and the Maritime Forest Limit in the Outermost Archipelago of Stockholm

The excursion took place on July 13th and started by buses from Stockholm across the island of Värmdön to Stavnäs, and continued by 3 big mine-sweepers from the Royal Swedish Navy to the small island of Långskär, in the archipelago of Björkskär.

I. The conifer forest region with oak was traversed both by the bus route and by the boat route from Stavnäs to the conifer forest limit in the outer Möja archipelago. The forest chiefly consists of *Pinus silvestris* (predominant especially on rocky ground) and *Picea abies*, with deciduous broad-leaved species immixed as single trees or small groves; southern thermophilous species as *Acer platanoides*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, and *Ulmus glabra*, and less demanding species, widely distributed also further north, as *Alnus glutinosa*, *Betula pubescens* and *verrucosa*, *Populus tremula*, *Salix caprea* and *Sorbus aucuparia*.

II. The maritime birch forest region, which is developed only in the very broad and thin archipelago ENE. of Stockholm, was studied in the archipelago of Björkskär, especially during a stop of some hours in the primeval vegetation on the island of Långskär. *Betula pubescens* is the predominant tree on the gneiss rocks, forming small groves between large open rock areas. In the small boulder valleys between the rocky parts it is partly replaced by *Populus tremula* and in wetter places, especially near the

sea shore, by *Alnus glutinosa*. The southern deciduous broad-leaved trees mentioned above do not occur, nor are there *Pinus silvestris* and *Picea abies*, except some isolated trees and small groves which are looking rather battered due to their constant exposition to sea wind and salt spray.

The vertical zonation of the vegetation of the rocks is as follows:

A. Marine vegetation.

1. Sublittoral belt, or permanently submerged vegetation.

a. Lower sublittoral belt, or algal vegetation below the lower *Fucus* limit.

b. Upper sublittoral belt, or *Fucus vesiculosus* belt.

2. Hydrolittoral belt, or belt of summer-annual filiform algae, submerged by high water but laid bare by the low water of the spring. (No tide in this part of the Baltic.)

B. Terrestrial vegetation.

1. Geolittoral belt, submerged by extreme high water on sheltered shores, and by storm waves on exposed shores.

a. Lower geolittoral belt, or *Verrucaria maura*-*Calothrix scopulorum*-belt.

b. Middle geolittoral belt, or *Caloplaca Lecanora*-belt.

c. Upper geolittoral belt, or *Lecanora atra*-*Rhizocarpon constrictum*-belt.

2. Epilittoral belt, never submerged, but influenced by atmospheric salt. Very rich rock lichen vegetation, alternating with patches of forest, dwarf shrub heath, grass heath, meadow, mire, etc.

III. The bare island region (without forest) was seen on the most exposed rocky points of Långskär and on small skerries outside this island. (See further Excursion Guide B 1.)

Leaders: Prof. G. Einar Du Rietz, Dr. Magnus Fries, Mr. Olov Hedberg, assisted by Miss Inga Arvidsson, Miss Karin Aschan, Mr. Ingmar Fröman, Mr. Lennart Holm, Mr. Måns Ryberg, Mr. Gunnar Wistrand, Miss Margareta Witting, Miss Karin Öblom, and others.

Participants: Prof. Robert Stephen Adamson, South Africa, Dr. Harry Howard Allan, New Zealand, Mrs. Valentine Allorge, France, Mr. Edvard Arney, Great Britain, Dr. Rimo Bacigalupi, U. S. A., Prof. Charles Baehni, Switzerland, Miss Philippa Barker, New Zealand, Mr. Jan Johannes Barkman, Netherlands, Prof. Robert Bauch, Germany, Mr. Rudolf Willem Becking, Netherlands, Prof. Faridoon Bharucha, India, Miss Ida Björnsson, Sweden, Dr. Kathleen Blackburn, Great Britain, Miss Gientje de Boer, Netherlands, Dr. B. K. Boom, Netherlands, Prof. Heinrich Borries, Germany, Miss Magda J. A. Boterenbrood, Netherlands, Prof. Arthur S. Boughey, Gold Coast, Dr. Elisabeth Boyko, Israel, Dr. Hugo Boyko, Israel, Mr. Antony Bradshaw, Great Britain, Dr. Josias Braun-Blanquet, France, Mr. G. Brebion, France, Prof. William Brown, Great Britain, Miss Isobel Victoria Burwash, Canada, Miss Ulla Bärlund, Finland, Dr. Tyge W. Böcher, Denmark, Mrs. Kirsten Böcher, Denmark, Dr. Carl Vilhelm Cedercreutz, Finland, Prof. Valentine Jackson Chapman, New Zealand, Dr. Pierre Chouard, France, Dr. Kafiluddin Ahmad Chowdhury, India, Dr. William Clark, Great Britain, Prof. Arthur R. Clapham, Great Britain, Miss Ann Conolly, Great Britain, Mr. Anders Danielson, Norway, Prof. Roger David, France, Miss Elisabeth Davies, Great Britain, Mr. Ieuan Davies, Great Britain, Mr. Wm. Ellis Davies, Great Britain, Dr. Paul Otto E. Dorff, Germany, Mrs. Susanne Dorff, Germany, Prof. Rollo O. Earl, Canada, Mrs. Olga Earl, Canada, Dr. Frederick Earnshaw, Great Britain, Mr. L. Ekström, Sweden, Mr. Sven Eriksson, Sweden, Prof. Knut Faegri, Norway, Dr. Abraham Fahn,

Israel, Dr. Naomi Feinbrunn, Israel, Prof. Franz Firbas, Germany, Prof. Frans Florschütz, Netherlands, Dr. F. Raymond Fosberg, U. S. A., Mr. A. Fridmark, Sweden, Mrs. Marianne Fries, Sweden, Prof. Rob. E. Fries, Sweden, Mr. Sigurd Fries, Sweden, Dr. Erika E. Gaertner, Canada, Prof. Reginald Ruggles Gates, U. S. A., Prof. Henri Gaussen, France, Mrs. A. Nellie Gibby, Great Britain, Miss Mary Gibby, Great Britain, Dr. Hamish Boyd Gilliland, South Africa, Mr. Vilhelm Gillner, Sweden, Mrs. E. Caroline Gimmingham, Great Britain, Dr. Harry Godwin, Great Britain, Dr. Augustus Gorter, Netherlands, Prof. Marcel Guinochet, France, Dr. Thomas van der Hammen, Netherlands, Prof. Thomas M. Harris, Great Britain, Dr. Constance Hartt, U. S. A., Mr. André G. Haudricout, France, Mr. L. H. Hedin, France, Dr. Ilse Heuer, Switzerland, Mr. Charles Edvard Hubbard, Great Britain, Prof. Eric Hultén, Sweden, Mr. Torsten Håkansson, Sweden, Mr. Reinhold Ivarsson, Sweden, Dr. Johannes Iversen, Denmark, Prof. Clément Jacquot, France, Dr. Jaakko Jalas, Finland, Mrs. Gladys James, Great Britain, Prof. Knud Jessen, Denmark, Mrs. Ingrid Jessen, Denmark, Mr. Paul Jovet, France, Mrs. Suzanne Jovet-Ast, France, Miss Inger Juel, Denmark, Prof. Aarno Kalela, Finland, Dr. David Keek, U. S. A., Prof. Mauno Johannes Kotilainen, Finland, Mrs. Saimi Maria Kotilainen, Finland, Prof. Viljo Kujala, Finland, Mr. Anders Olof Kylin, Sweden, Prof. Herman J. Lam, Netherlands, Dr. Joseph Lanjouw, Netherlands, Mrs. J. Lanjouw, Netherlands, Mrs. Doris W. Laycock, New Zealand, Mr. Olli Ensio Lehtonen, Finland, Dr. Johannes Lid, Norway, Mr. Axel Liljedahl, Sweden, Mr. Kaarlo Johannes Lounamaa, Finland, Dr. Alicia Lourteig, Argentina, Dr. Werner Lüdi, Switzerland, Mrs. Leni Lüdi, Switzerland, Dr. Åskell Löve, Iceland, Dr. Doris Löve, Iceland, Mr. Jack Major, U. S. A., Prof. Irene Manton, Great Britain, Prof. Friedrich Markgraf, Germany, Dr. Gunnar Marklund, Finland, Prof. Hans Melchior, Germany, Dr. Francis Merton, Great Britain, Prof. Herman Meusel, Germany, Dr. Peter

Michaelis, Germany, Prof. John T. Middleton, U. S. A., Dr. Peitsa Mikola, Finland, Mr. Georg Francis Mitchell, Eire, Mrs. Alma L. Moldenke, U. S. A., Dr. Harold N. Moldenke, U. S. A., Prof. A. Monoyer, Belgium, Prof. René Morquer, France, Prof. Kurt Mothes, Germany, Miss Ingrid Müller-Liebenau, Germany, Prof. Wolfgang Müller-Stoll, Germany, Mr. Fritz H. Möller, Denmark, Dr. Mina Nadel-Schiffman, Israel, Prof. Giovanni Negri, Italy, Dr. David James Donald Nicholas, Great Britain, Mr. Robert Noel, Great Britain, Mrs. Birgitta Norrans, Sweden, Mr. Gunnar Olsson, Sweden, Mr. Max v. Oosten, Netherlands, Mr. Fredrik Paludan, Sweden, Prof. William H. Pearsall, Great Britain, Mr. Bengt Pettersson, Sweden, Mrs. Anna-Greta Pettersson, Sweden, Prof. Beniamino Peyronel, Italy, Prof. Rodolfo E. G. Pichi-Sermolli, Italy, Prof. Arthur Pisek, Austria, Dr. Erling Porsild, Canada, Prof. Henri Prat, Canada, Dr. John Ramsbottom, Great Britain, Mr. Marcel Raymond, Canada, Dr. Karl Heinz Reching, Austria, Prof. Constantin Regel, Switzerland, Mrs. Edit Robinson, Great Britain, Prof. Walter Robyns, Belgium, Miss Isobel Rogerson, Australia, Prof. René Rol, France, Mr. Frank Eric Round, Great Britain, Dr. Jacques Rousseau, Canada, Mr. Pieter van Royen, Netherlands, Prof. Eduard Rübel, Switzerland, Dr. Walter Rytz, Switzerland, Prof. Walther Rytz, Switzerland, Prof. T. S. Sadasivan, India, Miss Edith Scamman, U. S. A., Prof. Elisabeth Schiemann, Germany, Mr. Erling Schønning, Denmark, Prof. Emil Schmid, Switzerland, Miss A.-L. Samuelsson, Sweden, Dr. Bernice G. Schubert, U. S. A., Mrs. Brita Schwank, Finland, Mr. H. K. A. Shaw, Great Britain, Dr. Wilhelm Simonis, Germany, Miss Nettie Stiebel, Israel, Prof. Harold St. John, Hawaii, Mrs. Harold St. John, Hawaii, Prof. Otto Stocker, Germany, Mr. Carl Volkmar Stoy, Sweden, Mr. Herbert Straka, Germany, Dr. C. V. Subrahmanyam, India, Dr. Thorvald Sørensen, Denmark, Dr. Niilo Söyrinki, Finland, Mrs. Annikki Söyrinki, Finland, Mr. Jaan Terasmäe, Sweden, Dr. Friedrich Thiergart, Germany, Prof. Georg Friedrich Leopold Tischler, Ger-

many, Mrs. Gisela Tischler, Germany, Miss Mary A. Todd, Great Britain, Dr. Jean Trochain, France, Prof. Carl Troll, Germany, Dr. William Bertram Turrill, Great Britain, Prof. Thomas Gaskell Tutin, Great Britain, Prof. Reinhold Tüxen, Germany, Dr. David Henriques Valentine, Great Britain, Mrs. Joan Winifred Valentine, Great Britain, Dr. Hervid Valin, Sweden, Prof. Lydia Walsh, U. S. A., Prof. Heinrich Walter, Germany, Prof. David Webb, Eire, Prof. Erich Werdermann, Germany, Miss Majorie Wilkins, Australia, Miss Camilla Wilske, Sweden, Miss Ulla Witt, Netherlands, Dr. Michael Zohary, Israel.

G. EINAR DU RIETZ

B2: Licheno-Bryological Excursion to the Island of Runmarö in the Stockholm Archipelago

The excursion departed from Stockholm by bus to Stavsns in the morning of July 13th and continued by boat to Styrsvik, on the west side of Runmarö. The day was spent on Runmarö and the group returned to Stockholm in the evening.

Lichenological section. This excursion intended to demonstrate the lichen flora and vegetation of the innermost part (the coniferous region) of the Archipelago with special regard to the influence of the varying rock ground (calcareous and siliceous rocks).

The group walked from Styrsvik via Uppeby to Nore on the eastern side of the island and took the same way back to Styrsvik. Some rare species of lichens were demonstrated on that occasion (*Dermatocarpon rivulorum*, *Cladonia elongata*, *Cornicularia normoerica*, a single specimen, etc.). (See further Excursion Guide B 2.)

Leader: Dr. Gunnar Degelius.

Participants: Dr. S. Ahlner, Sweden, Dr. O. Almborn, Sweden, Dr. V. Grummann, Germany, Prof. Grace Howard, U. S. A., Prof. E. Häyrén, Finland, Mrs. Ann-Marie Häyrén-Malmström, Finland, Dr. R. Maas Geesteranus, Netherlands, Dr. A. H. Magnusson, Sweden, Dr. F. Mattick,

Germany, Mr. P. G. Ozenda, Algeria, Mr. H. Runemark, Sweden, Dr. C. Tavares, Portugal.

Bryological section. The bryological excursion had a similar aim as that of the lichenological, i.e. to show the influence of varying rock ground on the moss vegetation. The group walked across the island in the south-eastern direction from Styrsvik where they returned in the afternoon. The vegetation on some calcareous rocks in the coniferous forest west of Vitträsk appeared to be of special interest. As the moss flora of the island is very little known, a number of species, new for that island, could there be collected. They were as follows: *Anomodon longifolius*, *A. viticulosus*, *Campylopus clodes*, *Ctenidium moluscum*, *Dicranum robustum*, *Eurhynchium Zetterstedtii*, *Neckera complanata*, *Thamnium alopecurum* and *Zygodon rupestris*. (See further Excursion Guide B 2.)

Leader: Dr. Edvard von Krusenstjerna.

Participants: Mr. A. H. G. Alston, Great Britain, Mr. P. Bell, Great Britain, Miss Dorothy Bexon, Great Britain, Dr. H. Buch, Finland, Dr. D. Catcheside, Great Britain, Miss Margaret Fox, Great Britain, Dr. O. Gjaerevoll, Norway, Miss Elsa Hallesjö, Sweden, Mr. S. Hansen, Sweden, Prof. K. Höfler, Austria, Mr. J. Kucyniak, Canada, Mr. M. Køie, Denmark, Mr. W. Meijer, Netherlands, Mr. A. Munk, Denmark, Mrs. Ruth Munk, Denmark, Mr. R. Parker, Great Britain, Dr. Irmentraud Raschendorfer, Austria, Prof. P. E. Richards, Great Britain, Miss Berit Sandström, Sweden, Prof. Geneva Sayre, U. S. A., Dr. H. Sjörs, Sweden, Dr. R. Tuomikoski, Finland, Mrs. Tellervo Tuomikoski, Finland, Dr. E. Warburg, Great Britain, Prof. R. van der Wijk, Netherlands.

GUNNAR DEGELIUS and
EDVARD VON KRUSENSTJERNA

B 3: General Algological and Lichenological Excursion to the Brackish Water of the Baltic

Sixty-nine members of the Congress took part in the tour on July 13th, designed to illustrate the vegetation living in and influenced

by the brackish water of the Gotland Sea at the outermost fringe of the Stockholm Archipelago at Huvudskär. (See Excursion Guide B 3 and C III a, and Acta Phytogeogr. Suecica, 30.)

Leaders: Mr. M. Wærn (algae), Mr. R. Santesson (lichens) and Mr. H. Luther (water phanerogames and *Characeae*).

Participants: Dr. A. A. Aleem, Egypt, Miss Joan Bain, Great Britain, Dr. Helen Blackler, Great Britain, Prof. H. L. Blomquist, U. S. A., Prof. T. Braarud, Norway, Prof. J. Brunel, Canada, Mrs. Susanne Brunel, Canada, Mrs. Marguerite Bulman, Great Britain, Dr. Elsie Burrows, Great Britain, Prof. F. Bustinza, Spain, Prof. A. Caballero, Spain, Prof. M. Chadeaud, France, Mrs. Anna Chadeaud, France, Prof. R. E. Cleland, U. S. A., Dr. E. Dahl, Norway, Mrs. Johanne Dahl, Norway, Dr. E. Y. Dawson, U. S. A., Prof. Th. Diannelidis, Greece, Miss Carola Dickinson, Great Britain, Dr. Kathleen Drew Baker, Great Britain, Prof. W. G. Fearnside, Great Britain, Prof. J. Feldmann, France, Dr. Geneviève Feldmann, France, Prof. F. E. Fritsch, Great Britain, Prof. H. Gams, Austria, Mrs. Marianne Grönberg, Sweden, Mr. A. Hagen, Norway, Mr. L. E. Henriksson, Sweden, Mrs. Elisabet Henriksson, Sweden, Mr. E. Holsinger, Ceylon, Prof. J. H. Johnson, U. S. A., Mrs. Merle Johnson, U. S. A., Mrs. Greta Koraa, Sweden, Dr. Josephine Th. Koster, Netherlands, Dr. T. Levring, Sweden, Mrs. Elsa Levring, Sweden, Dr. R. Lewin, Great Britain, Mrs. Joyce Lewin, Great Britain, Dr. Margaret Madge, Great Britain, Miss Lucy B. Moore, New Zealand, Dr. Betty Moss, Great Britain, Miss Aina Nilson, Sweden, Prof. H. Osvald, Sweden, Prof. G. F. Papenfuss, U. S. A., Dr. Mary Parke, Great Britain, Miss Hilda Parkes, Eire, Miss Elena Paunero, Spain, Mr. B. Peters, Sweden, Dr. H. Pitschmann, Austria, Mr. H. Th. Powell, Great Britain, Prof. E. G. Pringsheim, Great Britain, Mrs. Olga Pringsheim, Great Britain, Mr. G. Schotter, Algeria, Mr. W. V. Schowalter, U. S. A., Prof. H. Skuja, Sweden, Prof. E. Steemann Nielsen, Denmark, Dr. S. Suneson, Sweden, Prof. W. R. Taylor, U. S. A., Mrs. Stina Wærn, Sweden, Mr. F.



F. T. WAHLEN.

Photo: Uppsala-Bild.



M. J. SIRKS.

Photo: Dagens Bild.



F. VERDOORN.

Photo: Dagens Bild.



F. W. WENT.

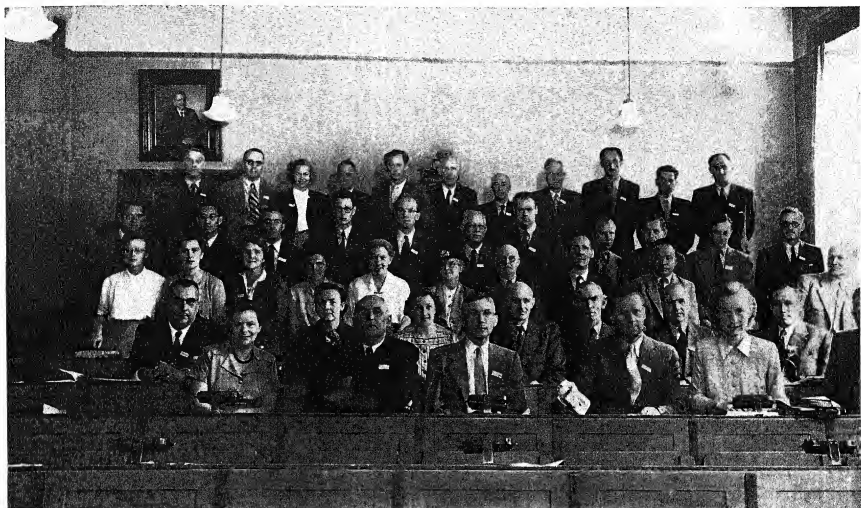
Photo: Dagens Bild.



V. N. SUCATJEV (to the right) and I. E. GLUSCHENKO, placing a wreath from the Soviet Delegation on the tomb of Linnæus in Uppsala Cathedral. Photo: Uppsala-Bild.



ELIAS MELIN places the wreath from the Congress on the tomb of Linnæus in Uppsala Cathedral. Photo: Uppsala-Bild.



Section Agronomy. In the first row, W. HERTZSCH (the fourth from the left), Mrs. MARGOT RUDOLF-LAURITZEN (fifth). In the second row, F. T. WAHLEN (4), J. M. POEHLMAN (6), HUGO OSVALD (7). In the third row, Miss MARY D. GLYNNE (3), F. R. HORNE (8), I. GRANHALL (10). In the fourth row, M. PLAUT (6).

Photo: E. Boldt-Christmas.



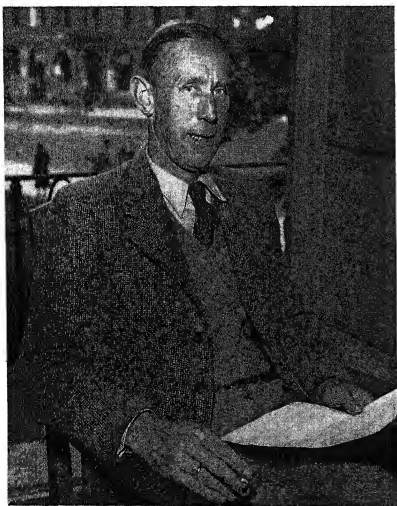
Section Paleobotany. In the middle of the first row, the President of the Section H. HAMSHAW THOMAS. On his left side (to the right) SUZANNE LECLERCQ, W. GOTHAN, W. J. JONGMANS, R. KRÄUSEL. On his right side (to the left) Mrs. SAVITRI SAHNI, T. G. HALLE, R. POTONÉ. The section recorder R. FLORIN is seen immediately behind R. KRÄUSEL; on his right side (to the left) J. WALTON, C. A. ARNOLD.

Photo: E. Boldt-Christmas.



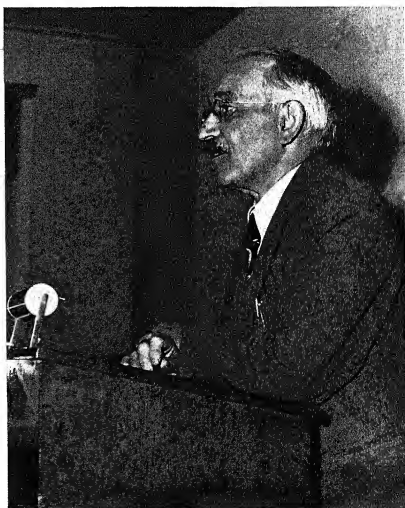
Section Nomenclature. In the first row, from the right: T. A. SPRAGUE, Miss ALICE EASTWOOD, E. D. MERRILL, J. LANJOUW, Mrs. M. L. SPRAGUE, W. ROBYNS, J. MATTFELD, B. P. G. HOCHREUTINER, H. HUMBERT.

Photo: Dagens Bild.



J. LANJOUW.

Photo: Pat, Stockholm.



SELMAN A. WAKSMAN.

Photo: Svenskt Pressfoto, Stockholm.



Section Phytogeography. In the front row, from the left: W. LÜDI, J. BRAUN-BLANQUET, R. TÜXEN, W. KOCH, C. TROLL, G. E. DU RIETZ.

Photo: E. Boldt-Christmas.



Palynological Conference. In the first row, G. ERDTMAN (the sixth from the left), H. A. HYDE (7), R. POTONIÉ (8), F. FIRBAS (9), and H. GODWIN (10). In the second row, extreme left, J. IVERSEN and K. Fægri. The fifth from the left is P. W. THOMSON, the seventh F. FLORSCHÜTZ. In the third row, extreme right, N. POLUNIN; next to him O. A. DAHL.

Photo: Wretmarks, Stockholm.



Mrs. NANNA FRIES, Mrs. BIBBI ÅBERG and Mrs. GERD STÅLFELT during one of the excursions arranged for the ladies.

Photo: Dagens Bild.



H. R. H. the Crown Prince of Sweden shakes hand with P. CHOUARD.

Photo: Dagens Bild.



"Under the Stockholm bridges." Entertainment for the ladies.

Photo: Dagens Bild.



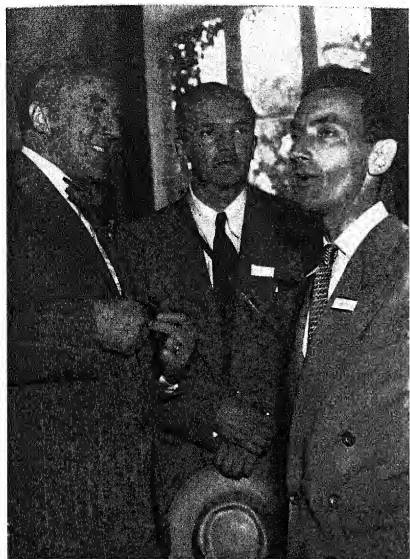
OLAVI MEURMAN, C. D. DARLINGTON and F. C. BAWDEN at Drottningholm Castle.

Photo: Dagens Bild.



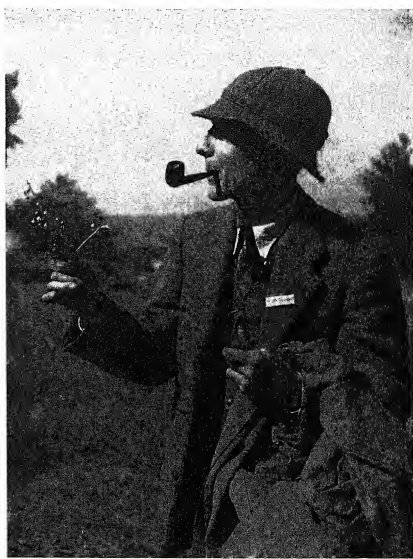
Egyptian delegates at Drottningholm Castle.

Photo: Dagens Bild.



ERIO HULTÉN, J. BRUNEL and M. RAYMOND.

Photo: Dagens Bild.



K. TH. CARTWRIGHT with *Linnaea borealis* on Utö, Stockholm Archipelago.

Photo: Dagens Nyheter.



G. TURESSON with a group of visitors in the Botanical-Genetic Garden of the Royal Agricultural College at Uppsala.

Photo: Uppsala-Bild.



A. F. BLAKESLEE and Miss MARY D. GLYNNE at Näs-Åker in northern Sweden (Excursion CI). In the background ERNEST SPRAGUE.
Photo: Ewert Åberg.



J. A. NANNFELDT and Mrs. CARIN EKLUNDH-EHRENBORG.
Photo: Dagens Bild.

G. E. DU RIETZ, Miss MARGARETA WITTING and WIM. MEIJER studying the vegetation of Komosse during Excursion A II b. Photo: Pressfoto, Jönköping.



N. SYLVÉN, Mrs. MAJ SJÖBERG, R. TUXEN, THOMAS KNOX WILSON and TORE ARNBORG during Excursion C III d. Photo: Östersunds-Posten.

Walker, Great Britain, Mr. T. Wennberg, Sweden, Dr. O. Wetzell, Germany, Dr. Irene Wilson, Great Britain, Dr. F. Woodward, Great Britain, Mr. H. Zech, Germany, Prof. W. Zimmermann, Germany.

M. WÆRN

B4: Limnological Excursion to Lake Vitträsk, Runmarö, in the Stockholm Archipelago

The purpose of the excursion, which took place on July 13th, was to demonstrate the vegetation in the limestone lakes of the island of Runmarö. Lake Vitträsk, the largest and most representative lake of Runmarö, was chosen as the main demonstration object. On its southwestern shore, the plant zonation in exposed and sheltered sections was studied. Only little attention was paid, however, to the terrestrial and upper amphibious zones which are here characterized by one dry *Pleurozium Schreberi*-*Vaccinium Vitis-idaea*-*Pinus silvestris*-forest and one wet *Climacium dendroides*-*Filipendula Ulmaria*-*Alnus glutinosa*-forest. A more detailed demonstration was made of the middle and lower amphibious zones with their Magnocariceta (mostly *Carex elata*) and fragmentarily developed Parvocariceta, and of the aquatic vegetation, dominated by different types of aquatic reed-swamps (*Phragmites*, *Scirpus lacustris*, *S. Tabernaemontani*, *Typha angustifolia* and *T. latifolia*) as well as of mats of *Chara aspera* and *C. contraria*. Some of the participants remained there in order to study the lower algal flora and vegetation (mainly diatoms) while others proceeded to Kasviken, a little lake east of the southern end of Vitträsk. Kasviken is not described in the excursion guide. Although both Vitträsk and Kasviken are limestone lakes, their vegetation differs in significant respects. The characteristic features in the vegetation of Lake Kasviken ultimately depend upon the small area covered by the lake, its position in a depression surrounded by forest and the considerable sediment layers in the lakes. Lake Kasviken is almost filled up by

aquatic vegetation and there are hardly any areas of free water. Very luxuriant amphibious reed-swamps occur, mainly composed of the *Typha* species mentioned above, and there are large mats of *Chara aspera*, *C. globularis* v. *capillacea* and *C. aculeolata*, locally accumulated to banks in the water surface. The participants had a good outlook over the lake and its different plant societies from a rock protruding into free water. On the way back they stopped near the outlet in the south-western part of the lake for a demonstration of the beautiful plant zonation. Here the participants studied the vegetation of a small raised *Sphagnum parvifolium*-*Ledum palustre*-*Pinus silvestris*-bog, its direct and abrupt transition into a wet eutrophic swamp (characterized in the bottom-layer by *Cinclidium stygium*, *Sphagnum teres*, etc.; in the field-layer by *Carex appropinquata* and *C. elata*), and the gradual change of the latter swamp into the amphibious reed-swamps of the lake.

Leader: Mr. Henning Horn af Rantzien.

Participants: Mr. Artur Almestrand, Sweden, Dr. Johannes Boye Petersen, Denmark, Mrs. Gunvor Boye Petersen, Denmark, Mr. Tyge Christensen, Denmark, Dr. Elizabeth Flint, Great Britain, Mrs. Maj-Britt Florin, Sweden, Prof. B. P. Georges Hochreutiner, Switzerland, Mrs. E. Hochreutiner de Leiris, Switzerland, Dr. G. Hodge, U. S. A., Prof. Taco Hajo van den Honert, Netherlands, Mrs. A. Horn af Rantzien, Sweden, Dr. Harold Howard, Great Britain, Dr. Friedrich Hustedt, Germany, Mrs. Marie Hustedt, Germany, Mr. Peet Kaaret, Sweden, Prof. Walo Koch, Switzerland, Dr. Robert Kolbe, Sweden, Mr. Jan Christian Lindeman, Netherlands, Dr. Asta Lundh, Sweden, Dr. Gunnar Nygaard, Denmark, Mr. Sigurd Olsen, Denmark, Miss Ruth Patrick, U. S. A., Mr. Nils Quennerstedt, Sweden, Mr. Robert Ross, Great Britain, Mr. Arent Wilhelm Silversparre, Sweden, Mr. Philip Tallantire, Norway, Mr. Kuno Thomasson, Sweden, Mr. Serge Villeret, France, Prof. Wilhelm Vischer, Switzerland.

HENNING HORN AF RANTZIEN

EXCURSIONS AFTER THE CONGRESS

CI: Excursion to Middle Norrland

This excursion was arranged by the section of Agronomic Botany. The participants left Stockholm by train in the evening of July 21st and arrived at Sundsvall the next morning. The group continued by bus to the Horticultural School and Research Station at Söråker. The afternoon was spent at Arboretum Drafle, near Härnösand. On the following day, July 23rd, the excursion continued along the river Ängermanälven. The State Experiment Farm Offer, near Undrom, and the Farm Home Management School at Stöndar were visited in the morning. The rest of the day was spent studying plant breeding work at the Västernorrland Branch station of the Swedish Seed Association at Lännäs, Undrom, and crop production problems at the Estate of Holm, Björkä Bruk.

On July 24th the Branch Station of the Association for Forest Tree Breeding at Sundmo, Inforso, was visited in the morning. After a bus tour through a forest country the group arrived in the afternoon to the State Experiment Farm at Gisselås. Here special attention was given to the peat soil vegetation. In the evening the excursion arrived at the Farm School of Torsta, where the participants were accommodated during the days spent in the area around Östersund.

On July 25th different crop production and plant breeding problems in the area of Stor-sjön were studied. For that purpose the Farm School of Torsta, the Jämtland Branch Station of the Swedish Seed Association and Kungsgården on the island of Frösön were visited. Special attention was devoted to the wild flora of Frösön. In the evening, when the group was dining at the Jamtli Museum in Östersund, the crop production in Sweden was discussed, preceded by an introductory talk by Professor HUGO OSVALD.

On July 26th the excursion continued towards the mountain area and followed the main highway to Norway. Stops were made at Mr.

NILS PERSSON's farm in Trång, where the participants learnt about the breaking of new lands for farming, and at the Mountain Research Station at Medstugan, owned and managed by the County Agricultural Society of Jämtland. On this farm, located 20 kilometers from the Norwegian border, the crop production under very hard climatic conditions could be followed. Opportunities were offered to study the mountain flora of Jämtland. The bus tour ended at Duved in the evening and the excursion continued by train to Enaforsholm, a farm owned by the Royal Academy of Agriculture and located in the mountain region of Jämtland. It was intended to spend the day of July 27th studying the mountain vegetation around Enaforsholm, but heavy rain stopped these plans. Despite of the rain some participants went to Högåsen to study and collect mountain flowers. (See further Excursion Guide C. I.)

Leaders: Dr. Erik Åkerberg and Dr. Ewert Åberg.

Participants: Dr. Rudolf Bauer, Germany, Mrs. Ilse Bauer, Germany, Prof. Geoffrey E. Blackman, Great Britain, Director Albert F. Blakeslee, U. S. A., Miss Gientje de Boer, Netherlands, Dean Leland E. Call, U. S. A., Mr. Ieuan Davies, Great Britain, Mr. Wm Ellis Davies, Great Britain, Dr. Hendrik Douwes, Sudan, Dr. Mary Dilys Glynne, Great Britain, Dr. Frank R. Horne, Great Britain, Prof. Edgar Knapp, Germany, Mr. Leslie Larter, Great Britain, Dr. Lee Ling, U. S. A., Prof. K. O. Müller, Great Britain, Dr. Mina Nadel-Schiffmann, Israel, Mr. Raymond Alen Neve, Great Britain, Prof. Hugo Osvald, Sweden, Dr. John M. Poehlman, U. S. A., Mrs. Rose Poehlman, U. S. A., Prof. Wilhelm Rudolf, Germany, Mrs. Margot Rudolf-Lauritsen, Germany, Mr. Ernest Sprague, U. S. A., Dr. Arthur Stocker Thomas, Great Britain, Dr. Friedrich Wahlen, Switzerland, Prof. Fritz W. Went, U. S. A., Mrs. Bibbi Åberg, Sweden.

ERIK ÅKERBERG and EWERT ÅBERG

CII 1 and CII 2 (first part): Excursion to Upper Norrland

The program for this excursion in Västerbotten, which took place on July 21st and 22nd, centered around ecological field experiments by actual methods for treatment of natural vegetation. It included visits to an experimental forest, to a large undrained mire and to chemically fertilized plots on drained or undrained mires or in old spruce forest growing on mineral soil. On July 21st different forest types at Kulbäcksliden were demonstrated by Prof. L. G. ROMELL. Degerö Stormyr was visited and the drainage problem was discussed. This has been studied in detail by Prof. C. MALMSTRÖM. A series of experiments for studies of forest nutrition problems was demonstrated, as well as experimental plots on mires in which phosphorus, potassium and boron were lacking, and experimental plots on mineral soils where the amount of easily available nitrogen was a decisive factor for the growth of the trees. On July 22nd the oldest Swedish experiments with ash as fertilizer on the twin mires Norra and Södra Hällmyren were seen. These experiments showed a satisfactory growth after fertilizing with ashes—even today, 30 years after the fertilizing took place. This is especially the case with birch. The excursion continued along the Baltic shore with its fringe of *Alnus incana* and ended in Umeå in the evening. (See further Excursion Guide C II 1, C II 2 (first part).)

Leaders: Prof. L. G. Romell and Prof. E. Björkman.

Participants: Dr. Henriette V. Bartoo, U.S.A., Prof. W. Bavendamm, Germany, Prof. D. V. Baxter, U.S.A., Mr. Charles Beall, U.S.A., Dr. K. T. Cartwright, Great Britain, Dr. Elise Conway, Great Britain, Prof. R. O. Earl, Canada, Prof. E. Eide, Norway, Dr. W. P. K. Findlay, Great Britain, Dr. Helene Francke-Grosmann, Germany, Prof. G. Gassner, Germany, Prof. H. Gaussen, France, Dir. R. Guy, France, Dr. M. Haugberg, Norway, Prof. Hans H. Heiberg, Norway, Prof. S. O. Heiberg, U.S.A., Dr. T. Hof, Netherlands, Prof. T. van den Honert,

Netherlands, Dr. L. M. Hutchins, U.S.A., Dr. Edna Johnson, U.S.A., Mr. E. Jørgensen, Denmark, Prof. V. Kujala, Finland, Dr. O. Langlet, Sweden, Dr. J. T. Middleton, U.S.A., Prof. E. Mork, Norway, Dr. Mildred K. Nobles, Canada, Miss Dorothea Olivier, South Africa, Prof. A. J. P. Oort, Netherlands, Mr. M. S. Parry, East Africa, Dr. Elizabeth Peabody, U.S.A., Miss Bess Reed Peacock, U.S.A., Prof. W. H. Pearsall, Great Britain, Prof. B. Peyronel, Italy, Prof. E. Reinders, Netherlands, Dr. Cornelia A. Reinders-Gouwentak, Netherlands, Dr. E. Rennerfelt, Sweden, Dr. H. Robak, Norway, Prof. P. A. Roelofsen, Netherlands, Prof. R. Rol, France, Dr. K. Stapp, Germany, Prof. O. Stocker, Germany, Mr. C. O. Tamm, Sweden, Dr. H. Vallin, Sweden, Dr. H. H. van Vloten, Netherlands, Dr. Johanna C. Went, Netherlands, Miss Jetske de Zeeuw, Netherlands, Prof. H. Zycha, Germany.

L. G. ROMELL and E. BJÖRKMAN

CII 2 (second part): Excursion to Upper and Middle Norrland

This excursion continued the excursion C II 1 and C II 2 (first part) and took place between July 23rd and 27th. It started at Björna, sponsored by the Mo & Domsjö company. Old forests at various elevations were studied as well as the regeneration of such forests by different methods. A number of diseases on the trees were observed. On pine trees *Melampsora pini-torqua* and *Phacidium infestans* cause great economic losses every year.

Plants characteristic of the North Swedish forest area were demonstrated, e.g. at Skuleberget on July 24th. Relicts from a warmer climate than the present one are found there, among others *Corylus Avellana*, *Tilia cordata* and *Acer platanoides*.

The most important root rot fungi and other rot fungi were discussed during a visit to the pulp wood yard at Domsjö. Methods of controlling the rots were discussed, as well as the rôle of rots in lowering pulp quality.

On July 25th the excursion proceeded to Arboretum Drafle, where the members were the guests of Director RAGNAR KEMPE. This arboretum was started 60 years ago. Today approximately 100 species of conifers and 300 species of broad-leaved trees and shrubs are found there. After the visit to Arboretum Drafle the excursion continued to Sundsvall, where the Research Laboratory of the Swedish Pulp Company was visited.

On July 26th the group arrived at Östersund. In the area around this city a 40 year old provenance experiment on pine was shown. On July 27th the members climbed the barren-topped mountain of Åreskutan at Åre, where the vegetation was studied, despite very heavy rain. On the slope of Åreskutan the plant associations which are characteristic of different plant geographical regions may be distinguished in succession as the altitude increases from about 400 m at the bottom of the valley until the "regio alpina" is reached at an altitude of about 900 m. From Åre the excursion members returned to Stockholm. (See further Excursion Guide C II 2 (second part).)

Leaders: Prof. E. Björkman and Dr. O. Langlet.

Participants: Prof. D. V. Baxter, U. S. A., Prof. W. Bavendamm, Germany, Mr. C. Beall, U. S. A., Dr. K. T. Cartwright, Great Britain, Prof. R. Earl, Canada, Prof. E. Eide, Norway, Dr. W. Findlay, Great Britain, Dr. Helene Francke-Grosmann, Germany, Dir. R. Guy, France, Dr. M. Haugberg, Norway, Prof. H. Heiberg, Norway, Dr. Tryntje Hof, Netherlands, Prof. T. van den Honert, Netherlands, Dr. L. Hutchins, U. S. A., Dr. Edna Johnson, U. S. A., Mr. E. Jørgensen, Denmark, Prof. V. Kujala, Finland, Prof. J. Middleton, U. S. A., Prof. E. Mork, Norway, Dr. Mildred Nobles, Canada, Prof. J. Oort, Netherlands, Mr. M. Parry, East Africa, Dr. Elisabeth Peabody, U. S. A., Miss Bess Reed Peacock, U. S. A., Prof. B. Peyronel, Italy, Prof. E. Reinders, Netherlands, Dr. Cornelia Reinders-Gouwentak, Netherlands, Dr. E. Rennerfelt, Sweden, Prof. P. Roelofsen, Netherlands, Prof. L. G. Romell,

Sweden, Prof. O. Stocker, Germany, Mr. C. O. Tamm, Sweden, Dr. H. Vallin, Sweden, Prof. H. Zycha, Germany.

E. BJÖRKMAN.

C III a: Special Algological Excursion to the Brackish Water of the Baltic

Twenty-four members of the Congress took part in this tour, on July 21st-26th, to see the vegetation in sea water with a salinity of about 0.5 % in the Öregrund Archipelago, a transitional area (north of lat. 60° N and east of long. 18° E) between the Åland Sea and the Bothnian Sea. The excursion was designed to illustrate the change in the brackish water flora between the Baltic proper and the Gulf of Bothnia showing decreasing marine and increasing lacustrine components, as well as the different vegetation of the exposed rocky shores and the sheltered interior parts of the Archipelago with beginning lake formation. (Guide B 3 and C III a, and Acta Phytogeogr. Suecica, 30.)

Leaders: Mr. M. Wærn and Mr. H. Luther.

Assistant leaders: Mr. L. E. Henriksson and Mrs. Elisabet Henriksson.

Participants: Dr. E. Almqvist, Sweden, Prof. T. Braarud, Norway, Mr. T. Christensen, Denmark, Miss Carola Dickinson, Great Britain, Mrs. Maj-Britt Florin, Sweden, Mr. T. Hasselrot, Sweden, Mr. E. Holsinger, Ceylon, Mr. O. Hotchkiss, U. S. A., Dr. Josephine Th. Koster, Netherlands, Mr. A. Martinsson, Sweden, Dr. Betty Moss, Great Britain, Mr. S. Olsen, Denmark, Dr. Mary A. Pocock, South Africa, Mrs. Daisy Pollard, Great Britain, Mr. H. Th. Powell, Great Britain, Dr. E. Pringsheim, Great Britain, Mrs. Olga Pringsheim, Great Britain, Mr. R. van der Veen, Netherlands, Mrs. Stina Wærn, Sweden, Mr. K. Ödegård, Norway.

M. WÆRN

C III b: Limnological Excursion to Lakes in Upland and Dalarna

The aim of the excursion was to show the participants the vegetation of a set of Swedish lakes and the nature of their surroundings.

The excursion was made by bus and lasted five days (July 21st-25th).

The first day was devoted to the study of different parts of Lake Mälaren. A visit was made to see the rich occurrence of *Viscum album* at Ådö, which is surrounded by large water areas. The appearance of *Viscum* in many localities in the region of Lake Mälaren is the most remarkable evidence of the influence of the lake on the local climate. Two bays of the lake with very different character were seen: Lilla Ullvifjärden, which is almost closed off from the rest of Lake Mälaren, surrounded by coniferous forests, deep and with steep shores. Yet *Oscillatoria*-plankton occurs there and many of its phanerogams are clearly eutrophic. Hjälstaviken is surrounded by large areas of arable land, is very shallow and has a very rich phanerogamic vegetation as well as a rich bird life.

The next day Lake Siggeforasjön (about 25 kilometers NW of Uppsala), one of the very few *Lobelia*-lakes in the province of Uppland was visited. In the lowered Lake Hallaren, on the boundary line between Uppland and Västmanland, notably *Nuphar pumilum* was studied, and on the shores *Scirpus radicans* and *Salix triandra*. After crossing the river Dalälven a stop was made at Lake Gruvsjön (circa 12 kilometers east of the town Hedemora). The northern part of the lake has been lowered about 13 meters and its earlier zones of erosion and sedimentation are open to inspection. The immigration of the vegetation shows interesting features.

The third day was devoted mainly to the study of the small but deep seepage lakes in the province of Dalarna. A trip was also made to the south-east precipice of the mountain Bisbergsklack, where several southern plants grow.

The following day some small lakes in the silurian region of Lake Siljan were visited. Lake Hosjön is surrounded by arable land, has a high content of electrolytes, dense reeds, and abundant phytoplankton. The meromictic Lake Storacksen is surrounded by sandy hills with

pine forest, has poor phytoplankton and clear water. It is a seepage lake, and so is Lake Tuv-tjärn. *Potamogeton filiformis* occurs in both of them. From Lake Siljan the excursion followed a south-eastern route through extensive forests to Gysinge near the boundary line between the provinces of Gästrikland and Uppland. At Gysinge the fine rapids of the river Dalälven were seen.

On the last day of the excursion the large, very shallow and moderately eutrophic Lake Tännaren was studied and the group followed its outlet to the coast. After having passed the small rivers Strömarån and Olandsån the group reached the Limnological Laboratory at Lake Erken which was demonstrated by Dr. W. RÖDHE. In the evening the party returned to Stockholm.

Leader: Dr. Gunnar Lohammar.

Participants: Dr. C. Cedercreutz, Finland, Dr. R. Kolbe, Sweden, Mr. F. Lundberg, Sweden, Mrs. S. Lundberg, Sweden, Miss I. Müller-Liebenau, Germany, Dr. W. Rodhe, Sweden, Dr. M. Schwickerath, Germany, Mr. A. Silfversparre, Sweden, Mr. K. Thomasson, Sweden, Mr. S. Villeret, France, Prof. E. Wassink, Netherlands, Mrs. L. Wassink-Van Lummel, Netherlands, Prof. D. Webb, Eire.

GUNNAR LOHAMMAR

CIII c: Phytogeographical Excursion to the Surroundings of Lake Torneträsk in Torne Lappmark (Northern Sweden), July 21st to August 2nd.

I. Railway journey
Stockholm—Abisko—Stockholm

A. The South-Swedish conifer forest region with oak. As to the tree species of this region, see Exc. B1. The northern border, or "the natural Norrland border", which was passed near Gävle, coincides with the northern limit of *Quercus robur* and many other southern plants, as well as with the southern limit of several northern plants.

B. The North-Swedish conifer forest region without oak.

1. *The North-Swedish Acer-Tilia-Corylus subregion.* This subregion was traversed in Gästrikland and southern Hälsingland. It occupies a narrow coastal zone up to northern Ångermanland, extending narrow arms into the lower river valleys. Many southern plants lacking in the other parts of North Sweden occur in this subregion, esp. at the foot of sunny precipices, e.g. *Acer platanoides*, *Tilia cordata* and *Corylus avellana*. Southern deciduous trees, esp. *Acer platanoides*, are predominant in the plantations of the towns etc.

2. *The North-Swedish Myrica subregion (without spontaneous Acer, Tilia and Corylus).* This subregion was traversed in northern Hälsingland, Medelpad, easternmost Jämtland, Ångermanland and Västerbotten. It forms an inland zone west of the previous subregion, and a narrow coastal zone to the north. Many southern plants are found here which occur also in the *Acer-Tilia-Corylus* subregion but are lacking in the subsequent subregions, e.g. *Myrica gale* (common and abundant), *Alnus glutinosa*, *Calla palustris*, *Rhynchospora alba*. *Betula* is predominant, and southern deciduous trees are rare in the plantations of the towns.

3. *The Central North-Swedish conifer forest subregion.* This subregion was traversed in Norrbotten. It is very typical between Boden and Gällivare. It is much poorer in southern plants than the previous subregion, but still contains many southern plants lacking in the next subregion, e.g. *Betula verrucosa*, *Salix aurita*, *Rhamnus frangula*. Grey willow scrub of northern species, esp. *Salix lapponum*, is much more common than in the previous subregions.

4. *The Prealpine conifer forest subregion.* This subregion differs from the one mentioned last by the still scarcer occurrence of southern plants and the greater abundance of mountain plants (esp. of grey willows). The often decreasing density of the conifer tree layer above a denser lower layer of birch trees, at least closely related to the mountain birch, *Betula pubescens* subsp. *tortuosa*, also gives a different character to the

region. The subregion is divided horizontally in two subordinate subregions, one where both pine and spruce occur—traversed by the railway between Gällivare (ca. 350 m above sea level) and Kiruna (ca. 500 m above sea level)—and another, more western subregion, with no occurrence of spruce—traversed by the railway between Kiruna and Abisko.

5. *The Subalpine birch forest region.* The railway ascends (max. height 551 m) into this region between Gällivare and Kiruna, Kiruna and Lake Torneträsk, and between Stenbacken and Abisko along the southern side of the lake. *Betula pubescens* subsp. *tortuosa* is the dominant tree species, mixed with or replaced by *Alnus incana* and *Salix nigricans* (coll.) in wet places.

II. Excursions in the Torneträsk district, with Abisko Östra (390 m above sea level) as headquarters

A. *The Pine forest region of the prealpine belt.* An outlier of this region and belt was studied in the central part of the Abisko Valley.

B. *The Subalpine birch forest region and belt.* This belt extends from the shore of Lake Torneträsk (342 m above sea level) up to ca. 650 m in the West and ca. 750–800 m in the East.

In the lower subalpine belt the birch forest is generally rather closed except for open areas caused by solifluction, mires, steep rocks, talus slopes, avalanches, etc. Besides the dwarf-shrub heath birch forests that cover most of the ground, with *Empetrum hermaphroditum* and *Vaccinium myrtillus* as main field layer dominants, there are meadow birch forests with tall herbs (*Geranium silvaticum*, *Trollius europaeus*, *Lactuca alpina* etc.). In extreme cases ferns (*Matteucia struthiopteris*, *Athyrium filix-femina* etc.) are predominant in the often very luxuriant field layer.

In the upper subalpine belt the birch forest is absent in large areas owing not only to the causes mentioned above but also to insufficient snow protection in winter or to late snow. The birch forest occupies only the optimal habitats and is often reduced to isolated patches or even

isolated trees or shrubs. The other vegetation is similar to that of the low-alpine belt.

This belt was visited on the slopes of many mountains on both sides of Lake Torneträsk.

C. The Low-alpine belt. In this belt there is no *Betula pubescens* subsp. *tortuosa*. Grey willow scrub of *Salix glauca*, *S. lapponum* and *S. lanata* covers large areas of moist ground in the lower parts of the belt, together with *Betula nana* scrub etc. But there is never a continuous willow scrub belt. The belt is best characterized as a dwarf-shrub heath belt. The poor heath vegetation of acid, non-calcareous soils usually covers most of the area, differentiated into 1) one *Empetrium* alliance (with *Empetrum hermaphroditum* and *Betula nana* as main dominants) on wind-swept hills, ridges and plateaus with no or unreliable snow cover in winter, 2) one *Myrtillion* alliance (with *Vaccinium myrtillus* as the main dominant and a characteristic species of the first order within the belt) in places well protected by snow in winter but laid bare early in the vegetation period, 3) one *Deschampsio-Anthoxanthion*-alliance (with *Deschampsia flexuosa* and *Anthoxanthum alpinum* as main dominants) in places with a snow cover lasting too long for the *Myrtillion*, and 4) one *Herbaceon* alliance (with *Salix herbacea* as its main dominant) on late snow patches. On calcareous soils this series is replaced by the rich heath vegetation: The *Empetrium* and the *Myrtillion* are replaced by different suballiances of one *Dryadion* alliance, with *Dryas octopetala* as its main dominant and characteristic species, together with *Cassiope tetragona*, *Rhododendron lapponicum*, and a great number of calciphilous grasses, sedges, and herbs. The *Deschampsio-Anthoxanthion* is replaced by the *Reticulato-Poion alpinae* alliance, with *Salix reticulata* and *Poa alpina* as main dominants, and the *Herbaceon* is replaced by the *Polarion* alliance, with *Salix polaris* as its main dominant.

In places with moving water in the ground these poor and rich heath alliances are replaced by meadow alliances. In the poor heath series the *Deschampsio-Anthoxanthion* alliance is replaced by an *Athyrium alpestre* alliance or by a

Ranunculo-Anthoxanthion alliance, with *Ranunculus acer* and *Anthoxanthum alpinum* as main dominants, or in lower parts of the belt by a *Trollio-Anthoxanthion* alliance (partly corresponding to the *Myrtillion*) with *Trollius europaeus*. The *Herbaceon* is replaced by a *Stellario-Oxyrion* alliance, with *Saxifraga stellaris*, *Oxyria digyna*, etc. as characteristic dominants. In the rich heath series the earliest snow-free parts of *Reticulato-Poion alpinae* are replaced by a *Potentilletto-Polygonion* alliance (with *Potentilla Crantzii* and *Polygonum viviparum* as characteristic dominants). The later snow-free parts of the same alliance are replaced by a *Ranunculo-Poion alpinae* alliance (with *Ranunculus acer* combined with many calciphytes) or in the lower parts of the low alpine belt with a *Trollio-Poion alpinae* alliance. The *Polarion* is replaced by an *Oppositifolio-Oxyrion* alliance with *Saxifraga oppositifolia* as a main dominant.

Mires are common both in the subalpine and in the low-alpine belt.

The upper limit of the low-alpine belt is drawn through the uppermost occurrences of *Vaccinium myrtillus*, which are usually found at ca. 1050–1100 m.

The low-alpine belt was visited on several mountains around Abisko and westwards to the Norwegian border.

D. The Mid-alpine belt. In this belt, much of the rich vascular flora of the low-alpine belt has disappeared, and has not been replaced by any new additions to the flora. *Cassiope tetragona* is the most important dwarf-shrub heath dominant even on rather acid soils, alternating with dwarfed and scattered *Betula nana*, *Empetrum hermaphroditum*, *Phyllococe coerulea*, *Vaccinium uliginosum* and *V. vitis-idea*, as well as with *Cassiope hypnoides*, *Salix herbacea* and *S. polaris*. Grasses (*Calamagrostis lapponica*, *Hierochloa alpina*, *Festuca ovina* and *vivipara*), sedges (*Carex Bigelowii* and *Lachenalii*) and the *Luzula*-species *arcuata* and *confusa* cover also much of the ground. The areas occupied by late snow vegetation, in extreme cases without any vascular plants, have increased, and large areas are also occupied by boulder fields covered

only by lichens and mosses. The upper border of the belt lies at ca. 1250–1350 m, or in the most sunny slopes 1400 m, and is marked by the disappearing of the last heath patches formed by *Cassiope tetragona*, *Vaccinium vitis-idaea*, *V. uliginosum*, grasses and sedges. The mid-alpine belt was studied by the excursion on several mountains south of the railway from Mt Nissontjärro SE of Abisko to Mt Vassitjåkko near the Norwegian border.

E. The High-alpine belt. In the lower parts of this belt, the dwarf willow sub-belt reaching up to ca. 1450–1500 m, or ca. 1600 m in the most favoured situations, *Salix herbacea* and *S. polaris* are still among the main field layer dominants on the small patches of soil suitable for vascular plants which occur in the immense boulder fields occupying most of the high alpine belt. Equally frequent are *Luzula arcuata*, *L. confusa* and *Ranunculus glacialis*. Other vascular plant species are very few and scarce, e.g. *Cardamine bellidifolia*, *Lycopodium selago* and *Poa arctica*. The dwarf willow sub-belt was visited by members of the excursion on the western mica-schist summits Mt Vassitjåkko and Mt Låktatjåkko and on the amphibolite summits Mt Tjåmohas, Mt Pallemtjåkko and Mt Nissontjärro south of Abisko. Only the last-mentioned summits reach the *Ranunculus glacialis* sub-belt, where the same vascular plants, except the dwarf-willows, occur on still more scattered patches. Only the extreme summit regions of the three mountains mentioned reach the pure lichen and bryophyte sub-belt without any vascular plants, but with the rich high alpine lichen and bryophyte vegetation still well developed and differentiated into several communities controlled by the duration of the snow-cover.

III. Railway journey Abisko–Narvik and boat trip into the Skjomen Fjord

On July 28th, the Excursions CIII c and CV joined each other. Between the Swedish-Norwegian border (Riksgränsen, 521.6 m) and Narvik the railway descends rapidly, entering the

pine forest belt at ca. 320 m. During a few hours stay at the southern end of Skjomen Fjord (Sørskjomen), the vegetation of the shore and of the lower mountain slopes was studied. (See further Excursion Guide C III c.)

Leader: Prof. G. Einar Du Rietz.

Assistant leaders: Dr. Olav Gjærevoll, Mr. Olov Hedberg, Mr. Nils Quennerstedt, Mr. Åke Persson, Mr. Olof Rune, Mr. Hans Runemark, Mr. Gustaf Sandberg, Miss Margareta Witting.

Participants: Prof. Henry des Abbayes, France, Dr. Anwar Abdel Aleem, Egypt, Dr. Harry Howard Allan, New Zealand, Mrs. Valentine Allorge, France, Mrs. Gienna Arseneau, U. S. A., Dr. George Avery, U. S. A., Miss Philippa Barker, New Zealand, Prof. Robert Bauch, Germany, Miss Dorothy Bexon, Great Britain, Dr. Hans Bode, Germany, Dr. Bernhard Boivin, Canada, Mrs. Cosette Boivin, Canada, Dr. B. K. Boom, Netherlands, Mrs. B. K. Boom, Netherlands, Dr. Elisabeth Boyko, Israel, Dr. Hugo Boyko, Israel, Dr. Clair A. Brown, U. S. A., Miss Jennifer Brown, New Zealand, Miss Isobel Burwash, Canada, Prof. Florencio Bustinza, Spain, Prof. Alberto Chiarugi, Italy, Dr. Clara Ciampi, Italy, Prof. Arthur Roy Clapham, Great Britain, Prof. Ralph Cleland, U. S. A., Miss Ann Conolly, Great Britain, Dr. Verona Conway, Great Britain, Prof. Robert Corillion, France, Prof. Roberto Corti, Italy, Mrs. Francini Corti, Italy, Mr. E. Dahl, Norway, Dr. R. F. Daubenmire, U. S. A., Mrs. Jean Daubenmire, U. S. A., Mr. J. Donner, Finland, Dr. A. Fahn, Israel, Dr. Mildred Faust, U. S. A., Dr. Naomi Feinbrunn, Israel, Dr. Elizabeth Flint, New Zealand, Dr. Raymond Fosberg, U. S. A., Dr. Margaret Fulford, U. S. A., Dr. Erika Gaertner, Canada, Prof. H. Gams, Austria, Prof. Ruggles Gates, U. S. A., Prof. Darnley Gibbs, Canada, Dr. Maud Godward, Great Britain, Dr. Augustus Gorter, Netherlands, Prof. Emilio Guinea, Spain, Mr. Camille Guinet, France, Prof. Marcel Guinocet, France, Mr. Erik Gummesson, Sweden, Dr. Thomas van der Hammen, Netherlands, Dr. Cornelia Harte, Germany, Dr. Constance Hartt, U. S. A., Dr. Ilse Heuer, Switzerland, Dr. Ilmari Hii-

tonen, Finland, Prof. Grace Howard, U. S. A., Dr. Bruno Huber, Germany, Dr. Friedrich Hustedt, Germany, Mrs. Marie Hustedt, Germany, Mr. Alexander William Jessep, Australia, Mrs. Dorothy Jessep, Australia, Mr. Paul Jovet, France, Mrs. Suzanne Jovet-Ast, France, Mr. Peet Kaaret, Sweden, Miss Mabel Kendall, Great Britain, Mr. James Kucyniak, Canada, Mr. Jan Lindeman, Netherlands, Dr. John Lund, Great Britain, Mrs. Hilda Canter-Lund, Great Britain, Mr. Jack Major, U. S. A., Mrs. J. Major, U. S. A., Miss Barbara Menzies, New Zealand, Prof. Albina Messeri, Italy, Prof. Herman Meusel, Germany, Dr. Peter Michaelis, Germany, Mr. Georg Francis Mitchell, Eire, Miss Lucy Moore, New Zealand, Mr. Alexis Moyse, France, Prof. Cornelius H. Muller, U. S. A., Prof. Wolfgang Müller-Stoll, Germany, Prof. Giovanni Negri, Italy, Mr. Robert Noel, Great Britain, Miss Dorothea Olivier, South Africa, Mr. Max van Oosten, Netherlands, Prof. Karl Paech, Germany, Prof. William Pearsall, Great Britain, Prof. Rodolpho Pichi-Sermolli, Italy, Prof. Arthur Pisek, Austria, Dr. Hans Pitschmann, Austria, Dr. Erling Porsild, Canada, Dr. Germaine Pottier, France, Dr. Immentraud Raschendorfer, Austria, Prof. Werner Rauh, Germany, Mr. Marcel Raymond, Canada, Prof. Walter Robyns, Belgium, Dr. Jacques Rosseau, Canada, Mr. Pieter van Royen, Netherlands, Prof. Walther Rytz, Switzerland, Dr. Walter Rytz, Switzerland, Prof. Francesco Sappa, Italy, Mrs. Maria Sappa, Italy, Mr. Charles Sauvage, Morocco, Prof. Emil Schmid, Switzerland, Prof. Flora Scott, U. S. A., Miss Dina Spierenburg, Netherlands, Prof. Harold St. John, U. S. A., Prof. Randolph Taylor, U. S. A., Dr. Friedrich Thiergart, Germany, Prof. Carl Troll, Germany, Prof. Frits Went, U. S. A., Prof. Erich Werdermann, Germany, Miss Ulla Witt, Netherlands, Dr. Michael Zohary, Israel.

G. EINAR DU RIETZ

CIId: Phytogeographical Forest Excursion to North Sweden

The excursion started in Stockholm, lat. N 59°20', on July 21st. Stops were made at several

places, where opportunities were given for closer studies, e.g. at Kratte Masugn, Torsåker, lat. N 60°30', in Gästrikland, Bjuråker in Hälsingland, lat. N 62°, Jorm in Jämtland on the Norwegian border, lat. N 64°45', Vallsjö in Southern Lappland, lat. N. 64°20', Muddus National Park, lat. N 67°, and Abisko, lat. N 68°25', where the excursion ended on August 5th.

During the excursion the participants got a survey of Norrland's forests, the never touched primeval forests as well as the cultivated forests; an insight was given into the varying forest types of Norrland, their stand composition, vegetation unions and soils.

During the visit to the primeval forests of Ankarvatnet climax woods of *Betula pubescens* were demonstrated. A vegetative regeneration of birch was found here, where a 2 1/2 yards high vegetation of among others *Aconitum septentrionale*, *Lactuca alpina*, and *Matteuccia struthiopteris* stopped the spruce seedlings. A list of higher plants from three places at Frostviken was made by the participants. It comprised 312 species.

At Vallsjö it was demonstrated how pine and spruce forest, when left undisturbed, generally changes into pure spruce wood, if the pine is not now and then exposed to forest fires.

Forests where the spruce does not grow, owing to too dry soil, and where the main association becomes a pine wood, were studied in Muddus. The oldest forests visited there had a pine generation 430 years of age.

At Abisko the group was offered the opportunity to see the most north-western Swedish pine wood and to discuss its regeneration. Two days were devoted to studies of the vegetation above the tree limit. (See further Excursion Guide C III d.)

Leaders: Dr. Tore Arnborg, and at Abisko Prof. G. Einar Du Rietz, Mr. Gustaf Sandberg and Miss Margareta Witting.

Participants: Dr. Jan Johannes Barkman, Netherlands, Mr. Rudolf Willem Becking, Netherlands, Dr. Howard Brewer, U. S. A., Dr. Evelyn Fernald, U. S. A., Mr. Eville Gorham, Great Britain, Dr. John Hislop Harrison, Great

Britain, Prof. Knud Jessen, Denmark, Mrs. Ingrid Jessen, Denmark, Prof. Robert McLean, Great Britain, Miss Denise Neugnot, France, Prof. Felix Rawitscher, Brazil, Mrs. Charlotte Rawitscher, Brazil, Prof. Constantin Regel, Switzerland, Mrs. Maj Sjöberg, Sweden, Dr. Mildred Southwick, U. S. A., Prof. Nils Sylén, Sweden, Prof. Reinhold Tüxen, Germany, Prof. Heinrich Walter, Germany, Mrs. H. Walter, Germany, Mr. Edvard Wibeck, Sweden, Mr. Thomas Knox Wilson, U. S. A.

TORRE ARNBORG

CIII e: Phytogeographical Excursion to Mire Districts in North Sweden

The excursion, which started from Stockholm on July 22nd and ended at Torneträsk near Abisko on August 7th, intended to give a section through the mire regions, as well as a more general idea of other kinds of vegetation in Northern Sweden. As only a small group took part in the excursion, there were excellent opportunities for a close study of the vegetation. During the first four days, which were spent in the province of Dalarna, mosses (bogs), fens and meadows were chiefly studied. The combinations of species in the meadows turned out to be very different from those of corresponding vegetation in Middle Europe, as pointed out by FIRBAS and LÜDI. The next four days, spent at Enafor in western Jämtland, were devoted to the mountains, the mountain valleys, and mires. Since it was raining continuously one could get a very good idea of the importance of "flushing" in this very humid countryside. Strongly sloping fens were flooded by ankle-deep streaming water, all small brooks were changed into vigorous torrents, and on Lake Änn, kindly demonstrated by Dr. LARS FAXÉN, only the topmost branches of the extensive willow thickets along the shores appeared above the water surface.

At Hammerdal, Central Jämtland, the calcicolous vegetation was studied. In Muddus National Park, Central Lappland, a tent camp was the headquarters during the studies of

primeval forest, mire, and lake vegetation. The last three days of the trip were spent at Abisko, with Prof. G. E. DU RIETZ, Mr. G. SANDBERG and Miss M. WITTING as guides, demonstrating the vegetation of the alpine, subalpine and upper conifer forest belts. The problem of the formation of *palses* (frozen peat-hillocks) was much discussed during the last of these excursion days. (See further Excursion Guide C III e.)

Leader: Dr. Hugo Sjörs.

Participants: Prof. Franz Firbas, Germany, Dr. Harry Godwin, Great Britain, Dr. Werner Lüdi, Switzerland, Mrs. Leni Lüdi, Switzerland, Dr. Georges Morel, France, Mr. Tage Roos, Sweden, Dr. Wilhelm Simonis, Germany, Mrs. Gunnel Sjörs, Sweden, Mr. Arvi Valmari, Finland, Prof. Lydia Walsh, U. S. A.

HUGO SJÖRS

CIV: Bryological, Lichenological, and Mycological Excursion to Jämtland

With some few alterations the planned programme as delineated in the excursion guide was realized, and most of the bryophytes and lichens mentioned there as well as a great number of other species were studied.

In the afternoon of July 21st the first part of the excursion started from Stockholm and arrived at Östersund in the evening. The 22nd of July the calcareous fens at Odensala and the conifer forests and mires at Mt Färskinnberget were studied; on the way back to Östersund a short stop was made at Brunflo church (*Letharia vulpina*-locality). On July 23rd the participants became acquainted with the flora of the southern slope of Åreskutan, but unfortunately the work was greatly hindered by heavy and numerous rain squalls. The same night the headquarters were moved to Storlien. During the four days (July 24-27) spent at Storlien the climate showed, unfortunately, too much of its oceanic features. Thus a rainfall of 124 mm was measured in three days (July 26-28); this is more than the mean precipitation of the whole month of July! In spite of the bad weather conditions, the flora of the alpine and

subalpine regions of Mt Stenfjeld and the spruce forests around Tevdalen (in Norway) were studied on July 25th, and an excursion to the Handöl water falls was also made (July 27th). The remaining two days at Storlien were devoted to short excursions in the neighbourhood to places most profitable for the mycologists, lichenologists, bryologists, and algologists.

The second part of the excursion had to start one day later than originally planned, because of dense mist and overflowed rivers. After having passed Blåhammarstugan (July 29-30) the weather improved and was particularly good when the top of Mt Storsylen was reached (July 31). The group returned to Handöl in the afternoon of the 3rd of August and departed from Storlien the following morning.

Among mycological observations the surprising finds of several hypogaeous fungi (at Oden-sala, Tevdalen, etc.) may be mentioned. As expected the lichenologists had the opportunity to study *Tholurna dissimilis* (Totthum-meln), *Cavernularia Hultenii* (Handöl, etc.), and *Lobaria Hallii* (Handöl), and several new and interesting finds were made. The bryologists recovered *Cololejeunea calcarea* (N. of Storlien), *Anastrepta orcadensis* (at the Norwegian boundary W. of Storlien), etc.

Leaders: Prof. J. A. Nannfeldt, Dr. E. von Krusenstjerna, Dr. H. Persson, Mr. R. Santeson (leader of the second part).

Participants: Dr. O. Almborn, Sweden, Dr. J. A. von Arx, Netherlands, Prof. N. Buchwald, Denmark, Mrs. Karen Buchwald, Denmark, Dr. Leontina Camici, Italy, Dr. M. Donk, Indonesia, Miss Margaret Feigley, U. S. A., Dr. Margaret Fulford, U. S. A., Dr. W. Groves, Canada, Mrs. Elsie Groves, Canada, Dr. V. J. Grummann, Germany, Mr. R. Grönblad, Finland, Mr. E. B. Hansen, Denmark, Dr. Lilian Hawker, Great Britain, Mr. L. Holm, Sweden, Dr. O. Jaag, Switzerland, Dr. I. Jörstad, Norway, Mr. M. Lange, Denmark, Mrs. Bodil Lange, Denmark, Miss Betty Legge, Great Britain, Miss Margit Liljestränd, Sweden, Mr. P. O. Lindahl, Sweden, Dr. R. Maas Geesteranus, Netherlands, Dr. A. H. Magnusson, Sweden, Dr.

G. W. Martin, U. S. A., Miss Aino Mathiesen, Sweden, Dr. F. Mattick, Germany, Mr. W. Meijer, Netherlands, Prof. A. Mix, U. S. A., Mrs. Katherine Mix, U. S. A., Mr. J. F. Morgan-Jones, Canada, Prof. R. Morquer, France, Dir. K. Müller, Germany, Mr. F. H. Möller, Denmark, Prof. Lilian Nagel, U. S. A., Mr. P. Ozenda, Alger, Mr. R. Parker, Great Britain, Dr. Tscharna Rayss, Israel, Prof. P. W. Richards, Great Britain, Prof. H. Richter, Germany, Prof. Geneve Sayre, U. S. A., Mr. A. M. Schotter, Algeria, Mr. G. P. Schotter, Algeria, Mr. E. Schotter, Algeria, Prof. M. Steiner, Germany, Miss Nettie Stiebel, Israel, Col. A. Ugglä, Sweden, Miss Grace Waterhouse, Great Britain, Prof. L. Wehmeyer, U. S. A., Mrs. Elaine Wehmeyer, U. S. A., Prof. R. van der Wijk, Netherlands.

J. A. NANNFELDT and R. SANTESSON

C V: Taxonomical Excursion to the Subalpine and Alpine Belts of Northern Lapland

The participants of Excursion C V left Stockholm together with those of Excursion C III c in a special train on July 21st and arrived at Abisko the following day. Quarters were taken at the Tourist Station. In the afternoon of the first day a part of Tour 2 of the guide-book was made. During the following days all tours described in the guide-book were performed, except Tour 3. Owing to unfavourable weather conditions Tours 7 and 9 had to be shortened. On July 28th a trip was made together with Excursion C III c to Narvik and Skjomen in Norway. The group departed from Abisko in the afternoon of August 2nd. (See further Excursion Guide C V.)

Most species mentioned in the description of the tours in the guide-book were seen, although, as was to be expected, some omissions proved inevitable.

On a mire close to the Research Station Dr. G. TAYLOR found plants of *Saxifraga Hirculus* L., a very remarkable find far from the known area of that species in the conifer-belt. It may be a remnant from a culture of species from

other parts of Lappland found in the same place about 1925, though it seems strange that such a conspicuous plant should not have been observed in the meantime in a place so often visited by botanists.

Leaders: Dr. E. Asplund, Dr. Axel Nygren.

Assistant leader: Mr. A. Fröman.

Participants: Mr. G. A. H. Alston, Great Britain, Mr. J. P. Anderson, U. S. A., Dr. Ch. Henriette Andreas, Netherlands, Dr. Ch. A. Arnold, U. S. A., Prof. L. Benson, U. S. A., Mrs. Inger Bohus Jensen, Denmark, Mr. R. Boutique, Belgium, Mr. R. Germain, Belgium, Mrs. A. Nellie Gibby, Great Britain, Miss Mary

Gibby, Great Britain, Prof. D. Gottlieb, U. S. A., Prof. H. E. Gregory, U. S. A., Mrs. Edna Gregory, U. S. A., Prof. W. Koch, Switzerland, Dr. Marcelle Le Gal, France, Dr. J. Lid, Norway, Prof. F. Markgraf, Germany, Dr. H. N. Moldenke, U. S. A., Mrs. Alma Moldenke, U. S. A., Miss Mary Percival, Great Britain, Dr. K. H. Rechinger, Austria, Dr. Bernice G. Schubert, U. S. A., Mr. Ch. Schweinfurth, U. S. A., Mr. N. D. Simpson, Great Britain, Prof. J. L. van Soest, Netherlands, Dr. G. Taylor, Great Britain, Prof. Th. G. Tutin, Great Britain, Dr. E. F. Warburg, Great Britain.

E. ASPLUND

DELEGATES AND ADDITIONAL MEMBERS

DELEGATES

After Communication No. 4 went to print on June 23rd 1950 the names of a number of delegates were sent to the Secretary General. The complete list of delegates is therefore given below.

Afrique Occidentale Française

Laboratoire de l'Office de la Recherche Scientifique d'Ostre-Mer à Adiopodoumé: *G. Mangenot*

Afrique Équatoriale Française

Institut d'Études Centre Africaines à Brazzaville: *J. Trochain*

Algérie

Institut Agricole d'Algérie: *A. Dubuis*
Société d'Histoire Naturelle d'Algérie: *P. Ozenda*
Université et Service de Recherches Botaniques,
Gouvernement Général d'Algérie: *Ch. Killian*

Argentina

Fundación Miguel Lillo: *H. R. Descole*
Museo e Instituto Nacional, Investigación de las Ciencias Naturales: *H. R. Descole*
Universidad Nacional de Tucumán: *H. R. Descole*

Australia

Linnean Society of New South Wales: *Mary Tindale*
Melbourne Botanic Gardens and National Herbarium: *A. V. Jessep*
Royal Society of Tasmania: *Winifred Mary Curtis*
University of Melbourne: *Ethel McLennan*
University of Queensland: *R. F. N. Langdon*
University of Tasmania: *Winifred Mary Curtis*

Austria

Zoologisch-Botanische Gesellschaft in Wien:
K. Höfler

Belgium

Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique: *P. Martens*
Jardin Botanique de l'État: *W. Robyns*
Koninklijke Vlaamse Academie van Wetenschappen, Letteren en Schone Kunsten van België: *W. Robyns*
Ministère de l'Agriculture: *W. Robyns*
Société Royale de Botanique de Belgique: *W. Robyns*
Université de Liège: *R. Bouillenne*

Brazil

Academia Brasileira de Ciências do Brazil: *F. Rawitscher*
Colegio Anchieta, Porto Alegre: *H. N. Moldenke*
Instituto Agronomico do Norte, Belem: *H. N. Moldenke*
Instituto de Botânica, São Paulo: *H. N. Moldenke*
Instituto Tecnológico, Rio Grande do Sul: *H. N. Moldenke*
Jardin Botânico, Rio de Janeiro: *H. N. Moldenke*
Museo Nacional: *L. E. de Mello Filho*
Museo Paranaense, Curitiba: *H. N. Moldenke*
Seção de Botânica, Instituto Marden, Ituitaba: *H. N. Moldenke*
Secretaria da Agricultura do Estado do Rio Grande do Sul: *Iwar Beckman*
Sociedade Botânica do Brasil: *F. Rawitscher*
Universidade de São Paulo: *F. Rawitscher*

Bulgaria

Bulgarian Academy of Sciences: *D. Jordanoff*

Canada

Canadian Phytopathological Society: *J. W. Groves*

Department of Agriculture: *J. E. Bier, B. Boivin, J. W. Groves, W. A. T. Hagberg, M. K. Nobles*

Fondation Marie-Victorin: *N. Poulvin, J. Rousseau*

Jardin Botanique de Montréal: *J. Rousseau*

McGill University: *M. V. Roscoe*

Ministère de l'Industrie et du Commerce, Province de Quebec: *J. Rousseau*

National Museum of Canada: *A. E. Porsild*

Royal Society of Canada: *J. Rousseau, R. D. Gibbs*

Université de Montréal: *J. Brunel*

University of Alberta: *L. P. V. Johnson*

University of British Columbia: *T. M. C. Taylor*

Chile

Instituto de Biología, Universidad de Concepción: *H. N. Moldenke*

Museo Nacional de Historia Natural: *J. Swallen*

Colombia

Universidad de Nariño: *H. N. Moldenke*

Costa Rica

Seccão Botânica, Museo Nacional: *H. N. Moldenke*

Cuba

Herbario, Colegio de la Salle, Vedado: *H. N. Moldenke*

Estación Experimental Agronómica, Santiago de las Vegas: *H. N. Moldenke*

Sociedad Cubana de Botánica: *A. Ponce de León y Aymé*

Denmark

Carlsberg Laboratorium: *Ö. Winge*

Foreningen til Svampekundskabens Fremme: *F. H. Möller*

Kongelige Danske Videnskabernes Selskab: *Ö. Winge*

Kongelige Veterinaer- og Landbohøjskole: *K. Gram*

Ecuador

Ecuadorian Institute of Natural Sciences: *M. Acosta-Solis*

Forest Department of Ecuador: *M. Acosta-Solis*

Egypt

Farouk I University: *M. Tadros, E. E. H. El-Shishiny, A. F. El Halaly*

Fouad I University: *Vivi Täckholm, Hussein Said*

Fouad I Agricultural Museum: *M. Drar*

Higher Institute of Agriculture: *A. El-Nayal*

Eire

Department of Agriculture: *T. J. Walsh*

Royal Irish Academy: *J. Doyle*

University of Dublin, Trinity College: *D. Webb*

Finland

Academia Scientiarum Fennica: *V. Kujala*

Centralutskottet för lantbrukets försöksväsen: *O. Meurman*

Finlands Lantbruksministerium: *O. Meurman*

Finnish Forest Research Institute: *V. Kujala*

Helsingfors Universitet: *A. Palmgren*

Societas pro Fauna et Flora Fennica: *A. Palmgren*

Societas Scientiarum Fennica: *S. Palmgren*

Societas Zoologica-Botanica Fennica Vanamo: *M. J. Kotilainen*

Statens Trädgårdsinstitut: *O. Meurman*

Turun Yliopisto: *H. Waris*

France

Académie de Sciences, Institut de France:

Roger Heim

Association Française pour l'Avancement des Sciences: *Roger Heim*

Conservatoire National des Arts & Métiers: *P. Chouard*

École Supérieure d'Application d'Agriculture Tropicale: *G. Noachovitch*

- Faculté des Sciences de Paris: *L. Plantefol, R. A. Buvat, J. Feldmann*
- Institut Français d'Afrique Noire: *Roger Heim*
- Institut National Agronomique, Paris: *G. Viennot-Bourgin*
- Institut National du Bois, Centre technique forestier tropical: *D. Normand*
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After Communication No. 4 went to print on June 23rd, 1950, a number of applications for membership in the Congress arrived. Some of these were printed on a loose sheet handed to the Congress members during the Congress. In order to make the list of members complete, those Congress members who were not listed in *Communication No. 4* are mentioned below.

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SESSION 1

July 12th, 2—4 p. m., Attendance: 20 members

Chairman: F. T. WAHLEN, *Recorder:* E. ÅKERBERG

SUBJECT:

Various Papers

C. REGEL (Zürich)

Pflanzenrohstoffe als botanisches und landwirtschaftliches Problem

Es gibt zwei ungeheure Rohstoffquellen auf der Erde, die in der Erde lagernden mineralischen Rohstoffe, wie Kohle, Erdöl, Metalle usw. und die in der Pflanzenwelt enthaltenen, die sogenannten pflanzlichen Rohstoffe, wie Pflanzenfasern, Pflanzenöle und Fette, ätherische Öle, vegetabilische Farben, Kautschuk, Guttapercha und Balata, vegetabilische Gerbstoffe, Drogen, Schleime und Harze, Saponine, Zellulose und Holz, Papiermasse, Kork, Gummiarten usw. Unter Pflanzenrohstoff verstehen wir alle in den Pflanzen enthaltenen Rohstoffe, die in der chemischen und mechanischen Industrie und im Gewerbe Verwendung finden. Während sich die mineralischen Rohstoffe allmählich erschöpfen, erneuern sich die pflanzlichen immerwährend und sind unerschöpflich. Auch liegt das Problem darin, sie so in den landwirtschaftlichen Prozess einzugliedern, dass sie keine zusätzliche für die Gewinnung von Nahrungsmitteln

benötigte Fläche einnehmen, sondern innerhalb des Fruchtwechsels mit anderen Pflanzen zusammen angebaut werden können. Das zweite Problem wäre für die Gewinnung von Rohstoffen liefernden Pflanzen wenn möglich nicht die fruchtbaren für die Nahrungspflanzen nötigen Flächen in Anspruch zu nehmen, sondern die für deren Anbau ungeeigneten Flächen sowie die Ödländereien, wie die Ödflächen der Gebirge, Moore, klimatisch ungünstige Gebiete, Wüsten usw. Hierbei würde gleichzeitig ein soziales Problem, Hilfeleistung der notleidenden Bevölkerung mancher Gegenden, wie z. B. der Gebirge, durch einträgliche hochwertige Kulturen auf wenig ertragreichem Boden, gelöst werden können. Hierfür müsste die Pflanzenzucht neue Wege gehen. Falls es für diese Zwecke keine passenden Pflanzen gibt, müssen solche auf der Grundlage einheimischer, Rohstoffe enthaltender, wildwachsender Pflanzen neu gezüchtet und die wildwachsenden, bisher wenig ertragreichen, domestiziert werden. Durch Beeinflussung und sachgemäße Behandlung und durch besondere Kulturmassnahmen liessen

sich die Erträge erhöhen. Ein weiteres Problem der Erhöhung der Wirtschaftlichkeit würde in einer mehrfachen Nutzung der Pflanzen liegen, d. h. in einer Nutzung, bei der aus ein und derselben Pflanze mehrere Rohstoffe gewonnen werden. Eine allseitige Durchforschung der ganzen Pflanzenwelt der Erde auf alle in ihr enthaltenen Rohstoffe hin und eine umfassende Planung und Rayonnierung auf bioklimatischer und wirtschaftlicher Grundlage müsste durchgeführt werden. Auch müsste ein eingehendes Studium der Möglichkeiten der Akklimatisation und der Naturalisation begonnen werden. Wegen der grossen wissenschaftlichen und praktischen Bedeutung der pflanzlichen Rohstoffe für Wissenschaft und Praxis und für die Landwirtschaft und die mit ihr verbundenen sozialen Probleme regt der Unterzeichnete die Gründung eines Internationalen Verbandes zum Studium und der Verwertung solcher Rohstoffe an, mit deren Vorbereitung begonnen worden ist, ein Projekt zu dem zahlreiche Zuschriften aus allen Weltteilen sich zustimmend geäußert haben. Der Verband sollte als ständige Sektion an den Internationalen botanischen Kongressen und an der IUBS (Union of Biological Sciences) organisiert werden.

Discussion

HUGO OSVALD: I want to support the proposals made by Dr. REGEL that at the next Botanical Congress a section for plant raw materials should be organized. I also agree with him that an association for plant raw materials would be of great value. I should, however, like to suggest that the scope of the association should be limited to the central parts of the knowledge of plant raw materials. It seems to me that the program of the association is becoming too wide if it should also include the problems of, for instance, plant breeding.

E. BOYKO: A new commission for applied ecology has been set up in the course of the sessions of the IUBS and Dr. BOYKO, its chairman, wants to organize immediately commit-

tees on some fields of research. On the list of the branches which he will take into immediate organisation is the one for ecology of industrial plants and I know that he intended to ask Prof. REGEL also to help and contribute to this work. I believe therefore that there are good prospects in the development of research on the lines pointed out and wished for in the lecture of prof. REGEL.

HAROLD ST. JOHN (Honolulu)

Origin of the Sustenance Plants of the Polynesians

The sustenance plants of the Polynesians consisted of 1 beverage plant, and 21 food plants of which 4 were not present in Hawaii in aboriginal times.

The place of origin of many of these cultivated species is unknown, for many occur only in cultivation, but it may be inferred from the area of aboriginal cultivation or from the ranges of their closest relatives.

Of American origin there is only *Ipomoea Batatas* which was called in Polynesia cognates of "kumar," a name of American Indian origin (Kechua tribe). The *Ipomoea* occurred in aboriginal times throughout Polynesia as far west as New Zealand and to central New Guinea. This species was lacking in Micronesia and in the central and western East Indies.

Originating in New Guinea was *Saccharum officinarum*; from the Solomons was *Musa Troglodytarum*; and from the Melanesian-Polynesian boundary was *Piper methysticum*:—making 3 species originating in the Central Pacific.

Originating in the Indo-Pacific are the remaining 18 species.

The vernacular names of the species give evidence of routes of migration of the food plants and the peoples who carried them. Seven species, though widely dispersed, have Polynesian names that are restricted to Polynesia, including Fiji, Nukuoro, and Kapingamarangi. Plants with vernacular names ex-

tending, as cognates, to the Western Pacific, to the Philippines, the Sunda Is., etc., total 13 species. One species, *Cocos nucifera*, was common throughout to the Indian Ocean and also had one vernacular name used in cognate forms from Hawaii to Madagascar. These cognate names give evidence, but the evidence does not prove the migration route of the people who carried them.

Travelling eastward along the Micronesian route, of the 18 species considered of Indo-Pacific origin, the following number of species are absent on the various islands or groups:

Marianas	6
Palau	6
Truk	3
Ponape	5
Kusaie	5
Marshalls	11
Gilberts	13

Travelling eastward along the larger islands of the East Indies, all of the 18 Indo-Pacific species are found to have been in aboriginal cultivation.

Evidence from the vernacular names, as identities or cognates, implies a western origin of all the Polynesian sustenance plants except one (*Ipomoea Batatas*), but it does not indicate the exact route. Evidence from the areas of aboriginal cultivation seems to settle the question. The island stepping-stones on the Micronesian route lacked from 1/3 to 2/3 of the crop plants. Since the islands of the East Indies route had all of the species of sustenance plants in aboriginal cultivation, it seems clear that this southern route must have been the migration route of the Polynesian peoples.

Discussion

A. C. SMITH: Congratulate speaker on lucid presentation of subject. It is noteworthy that his conclusions that the Polynesians entered their area through the new Guinea—Fiji chain of islands parallels conclusions of phyto-

geographers that the indigenous plants of the regions had this same primary route of migration.

HUGO OSVALD: How can you explain the occurrence of sweet potato on the eastern Pacific Islands unless you accept the theory presented by HEYERDAHL, i.e. that the people in the eastern Pacific came from South America and brought their food plants with them?

H. ST. JOHN: It is generally agreed that the sweet potato could not have crossed the Pacific Ocean itself, but that it must have been carried by people. The possible carriers were two, either the Peruvians or the Polynesians. The Peruvian Indians were wholly land-bound. They had no seaworthy boats, but only pirogues and rafts. There is no trustworthy historic record of any long maritime voyage by them. Fishermen on a raft could have been blown out to sea, and the currents might have taken it to Polynesia, but during the months required, without sufficient food and water, the men would have perished. Yet, it is still conceivable that a few raw sweet potatoes might have remained on the raft and have been drifted to the islands, though the possibility is very remote.

The other possibility is that the Polynesians visited Peru and returned with articles of trade or booty. The Polynesians coming from Asia crossed the Pacific to settle the far flung islands, now called Polynesia, occupying all the large islands from Tonga to Hawaii, Mangareva, and Easter. They were great mariners, and for 200 years made regular round trips between Hawaii and Tahiti. They navigated by astronomy and by sea and bird lore. Their temporary settlements have been found on almost every coral island and atoll of the eastern Pacific. Their voyaging canoes had twin hulls some 70 feet long, with a broad deck and a cabin. Sir Peter Buck has announced his theory that a Polynesian voyaging canoe from Mangareva or the Marquesas made the round trip in the 12th Century, reaching and tarrying in South America. A crew of 50 or so Polynesians, large and sturdy, drilled and experienced war-

rions could have made contact with the Peruvians at coast villages, traded for food and goods, and tarried unharmed because of their military strength. Dissatisfied with the arid, barren coast, they could have re-embarked for a homeward voyage, aided by the Humboldt Current. It seems possible and probable that the Polynesians carried the sweet potato from South America into Polynesia. None of the other food plants of the Polynesians were of American origin.

M. PLAUT (Rehovot)

Die Einführung von Sommerroggen als landwirtschaftliche Kultur in Israel

Palästina und der Middle East kennen fast keinen Roggenanbau. Wie bekannt wird in der Welt etwa 98–99% Roggen als Wintersorte angebaut und Sommersorten sind nur wenige gezüchtet worden; ausser der Sommerroggenzüchtung von Lochow, die auch von RÜMKER beschrieben wird, haben weitere Sorten keine grössere Bedeutung erlangt. Die Umzüchtung von Wintersorten von Weizen und Gerste in Sommerformen ist viel mehr in der Literatur beschrieben als die Eigenschaften von Sommerroggen.

Die Beobachtung, dass schwedische Sommerweizen (wie Diamant) 1937 in Palästina als Winterfrucht angebaut ganz gute Erträge geben, führte uns zum Versuch von Lochow, Petkus, und Vilmorin, Paris, Sommersaat von Roggen zu bestellen.

Nach anfänglichen Misserfolgen haben wir in einer Reihe von Palästina-Wirtschaften mit diesen Sorten (z. T. auch von der in Amerika und Italien benutzten Sorte Abruzzi italienischen Ursprungs, bezogen aus Tanganjika) Erträge pro Hektar in Israel von ca. 1000–1400 kg erhalten, bei guter Düngung 1700–2230 kg auch auf grösseren Flächen. Als Vergleich rechnen wir mit ca. 1300–1700 kg Weizen; maximale Erträge der Qualitätssorten 2500–3000 kg. Die Aussaat erfolgt November–Dezember. Die Regen hören Anfang April auf. Es folgt daraus, dass Sommerroggen

auf Sandböden mit nicht schlechteren Erträgen wie Weizen angebaut werden kann. Während in Europa Roggen im September, also ca. 6 Wochen vor dem Weizen in der Erde sein muss, säen wir im Dezember, das Schossen erfolgt im März, die Blüte im April, blütenphenologische Beobachtungen ergeben andere Blühstunden, zumal durch Chamsin beeinflusst wie in Europa. Die Ernte erfolgt Anfang bis Mitte Mai.

Der Roggen ist in Israel viel weniger empfindlich für Rost als der Weizen, der in Rostjahren schwere Verluste ergeben kann. Die Schwankungen der Ernten von Weizen sind viel grösser als in Europa.

Der Roggen erhält Ende Januar—Anfang Februar eine N-Düngung ohne Lagerneigung und ohne Rostbefall. Blüten- und Befruchtungsstörungen kommen vor, sie sind z. T. sortenbedingt, auch von der Herkunft abhängig; ferner können Hitzewellen und plötzliche Kälte im Vorfrühjahr den Ansatz der Frucht stören. Auslese ist notwendig, um Gleichmässigkeit der Ähren und Blütenbildung, volles Spreitzen der Blüten, Beobachtung der Freilassung des Blütenstaubes zu erreichen. Auf diese hat insbesondere zu späte Saat Einfluss.

Roggen wird in Algerien und Marokko in kleinen Flächen je ca. 2000–4000 ha angebaut, TH. GITHENS and E. WOOD (The Food Resources of Africa, Pennsylvania, Prep. Africa Handbooks 3, 1943. Philadelphia) geben Erträge pro Hektar an, 1934–1938:

	Roggen	Hafer	Gerste
Algier	430–870	650–950	480–770 kg/ha.
Marokko	190–590	540–1840	430–980 kg/ha.
Tunis		400–770	250–560 kg/ha.

Im Rif Atlas spielt Roggen in der Berberdiät eine Rolle. Auch WOOD denkt, dass Roggen ist "well adapted to conditions there," p. 71, i.e. Es scheint mir aber, dass es sich um in den Höhen gebauten Winterroggen dort handelt.

An 1000-Korngewicht haben wir im Mittel 20,9 g erhalten, nehmen aber an, dass sich durch Selektion von Sorte und Herkunft die

Zahl stark steigern lässt. Petkus Roggen enthielt 30–40 % grünblaue und 60–70 % gelb-braune Körner, in der Nachkommenschaft waren mehr grünblaue Farben, bei Vilmorin-saat waren 25–40 % grünblau mit der Neigung mehr gelb zu vererben.

Die Pollenkeimung ist schwierig.

Der Sommerroggen enthielt ca. 10 % Eiweiss und 1,65 % Fett.

Die Viscosität mit 0,02 n. Milchsäure bestimmt ergab keine Unterschiede gegenüber australischen und türkischen Weizen. (Versuche mit Ing. B. ZELSBUCH.)

Der Anbau wird auf leichten Böden in Israel fortgesetzt, ferner die Züchtung auf Herkunftsunterschiede betrieben, wir haben auch schweizer und spanische sowie amerikanische „Sorten“ erhalten, die Unterschiede in der Entwicklung zeigen. Einheitlich war keine Sorte. Interessant ist das Verhalten des Israel Sommerroggens bei Winteraussaat in Europa. Darüber liegen Erfahrungen noch nicht vor.

Die Möglichkeit des Sommerroggenanbaus ohne Bewässerung auf sandigen Flächen bei ca. 400–600 mm Winterregen zu ziehen, kann für die Getreidewirtschaft des Landes und Planung wichtig werden.

Discussion

F. T. WAHLEN: Im Hinblick auf die sehr wichtige Frage der Wasserversorgung in Meditterranklima, wollte ich den Referenten fragen, ob und in welcher Menge Gewässerungswasser gegeben wurde, um die genannten Erträge zu erzielen. Es gilt ja bekanntlich im

Getreidebau dieser Gebiete die kritische Periode von Ende März (Ende der Winterregenfälle) bis zur Ernte zu überbrücken.

OLOF SVANBERG: Es gibt Probleme, welche mit der interessanten Mitteilung von Prof. PLAUT prinzipiell zusammenhängen: 1.) Wie viele Hektar angebauter Nutzfläche stehen in Israel überhaupt zur Verfügung für Produktion von Lebensmitteln? 2.) Wie zahlreich ist die Bevölkerung Israels, welche wenn möglich mit den Lebensmitteln von dieser Anbaufläche versorgt werden müssen, d. h. wie ist die allgemeine Lebensmittellage? 3.) Welche landwirtschaftlichen Kulturpflanzen können auf den in Frage kommenden leichten Böden Israels überhaupt nebst dem Roggen gebaut werden?

MENKO PLAUT: We usually grow rye in Israel without irrigation, like wheat and other cereals. Irrigated areas in Israel have been doubled in the last years. The population is $1\frac{1}{2}$ million and cereals grown in Israel supply only 10–20 % of the needed amount. Suitable varieties of rye give average yields of $1-1\frac{1}{2}$ tons per hectare. We have found that a variety from Georgia (U.S.A.) is suitable for our purposes.

In the year 1951–52 the total area of field crops in Israel was 325 000 hectares, of these 45 000 were irrigated. The scheme for the next 10–20 years is to grow 425 000 hectares field and forage crops, 150 000 of these under irrigation, provided sufficient water pipes are available. On light soils in Israel irrigated *Citrus* groves, potatoes, pea-nuts and sweet potatoes are grown. Non-irrigated crops of light soils are barley, lupine and probably also rye and *Serradella*.

SESSIONS 2 AND 3

Jointly with Section PHF: July 14th, 9 a. m. — noon and 1–4 p. m., See pages 699 and 702

SESSION 4

July 17th, 9 a. m.—noon, Attendance: 100 members

Chairman: F. T. WAHLEN, Recorder: E. ÅKERBERG

SUBJECT:

Microbiological Problems

ARTTURI I. VIRTANEN (Helsingfors)
*Microbiology and Chemistry of Symbiotic
Nitrogen Fixation*

Nitrogen fixation in the leguminous root nodules is a phenomenon that arouses a most many-sided interest. In the first place it is fundamental to life upon the whole earth, because without this remarkable symbiotic fixation of atmospheric nitrogen life would be very poor and the development and existence of man hardly possible. The mechanism of the process is quite special as a chemical problem, as along with the elucidation of the fixation of molecular nitrogen and the enzyme system acting therein a question also arises as to how the nitrogen fixation is associated with the formation of carbon compounds in the photosynthesis. Biologists again are particularly attracted by the symbiosis between nodule bacteria and the host plant which is a necessary prelude to the nitrogen fixation. Chemical and biological aspects are linked together in the examination of the phenomenon to an extent often making them inseparable.

In this talk I am going to deal with some in my opinion central questions of nitrogen fixation in the leguminous root nodules, chiefly in the light of the investigations carried out in the Biochemical Institute in Helsinki. The involvement of chemistry in biology is striking in these studies. All of our researches of fundamental nature have been carried out in the sterile culture system mostly with peas. If a sterile culture solution, into which a sterile pea seedling is transferred, is inoculated with a strain of pea *Rhizobium*, nodulation begins

on the roots about 6–10 days after inoculation. For the examination of many questions application of a method of this type is necessary because in the pot experiments foreign bacterial strains or other micro-organisms may affect the results. I may mention here as an example specially the investigations which aim at the elucidation of the effectiveness of different bacterial strains. In pot experiments where the quartz sand used as growth medium as well as the pots themselves are sterilized before sowing, nodules begin to appear after some time in the roots of pea or clover growing without combined nitrogen, although neither the seed nor the growth medium are inoculated with the respective legume bacteria. Infection occurs by air or by contact. Therefore it is difficult to obtain nodule-free control experiments parallel with the inoculated ones. Such an infection may badly interfere with the results. I believe that the observations recorded in the literature on the change of ineffective bacterial strains to effective ones and *vice versa* by repeated passage through the host plant are in the first place ascribable to infection by other strains of *Rhizobium* than the one used for inoculation. In sterile cultures we have never noted such a change. For instance, our entirely ineffective strain of pea *Rhizobium* H VIII has constantly remained ineffective after many passages through the host plant.

Regarding the competition between different strains of *Rhizobium* in the nodule production, let me mention the following observations. In the earlier literature the idea was introduced that the first strain forming nodules

on the roots of the host plant calls forth a certain degree of immunity that prevents infection by other strains. Mostly, however, it was considered that after a poorer strain had formed nodules a more effective one could still induce further nodulation. The experiments in our laboratory by Mrs. LINKOLA have given the following results. A pea plant growing in the sterile culture system was inoculated with the ineffective strain H VIII and after the appearance of the first nodule re-inoculation was made with an effective organism, but in most cases no effective nodules were formed during many weeks and, naturally, the pea did not grow. In the clear nutrient solution used it was easy to observe the nodulation. The ineffective H VIII strain produced white round nodules, which were easy to distinguish from the reddish elongated nodules formed by the effective strains. Nodulation by H VIII continued at least for 6 weeks. Since, in spite of such a long period, the effective strains did not usually induce nodulation we concluded that the strain H VIII must have brought about some kind of resistance in the roots against other bacterial strains.

THORNTON advanced the idea that the bacteria first invading the roots do not cause any immunity but that the inability of the later inoculated strain to form nodules simply results from the fact that the first strain saturates the roots with nodules so that the second strain has no chance to produce nodules. This does not fit in with our observations because the strain H VIII continued to form nodules and in spite of that prevented nodulation by the effective strains. Only when the pea had almost entirely withered, a separate effective nodule might occasionally appear and a new shoot began to grow rapidly. It seems that different bacterial strains are able to compete with varying success with one another. In this respect the results obtained by us and at Rothamsted are in good agreement. It is clear that this question is of great importance in the selection of strains to be

used by farmers for inoculation. I may mention in passing that nowadays we arrange in the pot experiments controls by infecting the seed of pea at the time of sowing with H VIII strain whereby in most cases no effective nodules are formed by later infections, and the pea is unable to grow without nitrogen nutrition.

Between the effective and ineffective nodules we observed a distinct chemical difference in 1944. The former ones always contain red pigment, the latter ones never. The red pigment was identified by KUO as hemoglobin in 1939 and we confirmed his finding in 1944. This hemoprotein, which we call leghemoglobin, differs, however, essentially from the hemoglobin of blood as our studies have revealed. True, the hemin component is the same in both of them but the protein component is very much different in composition and properties. Leghemoglobin contains e.g. liberally isoleucine, which is not found in the blood hemoglobin, the histidine content of leghemoglobin is only about 3%, while that of blood hemoglobin is 12%. The isoelectric point of leghemoglobin is about pH 4.4, that of blood hemoglobin about pH 7. We have succeeded in separating electrophoretically highly purified leghemoglobin into two components whose isoelectric points are pH 4.4 (the faster) and 4.7 (the slower).

Leghemoglobin is present in the cytoplasm of the root cells which are full of bacteria. If the excised nodules are placed in water leghemoglobin is fairly rapidly diffused into it. According to our experiments leghemoglobin is indispensable to the nitrogen fixation because, besides the absence of leghemoglobin from the ineffective nodules, there is also otherwise a definite parallelism between the nitrogen-fixing ability and the leghemoglobin content of the nodules.

The function of the pigment in the nodules has not yet been solved for certain. The idea that leghemoglobin acts as a storer and a carrier of oxygen appears very natural since the oxygen supply of strongly aerobic bacteria in the nodule cells is very limited.

SCHMIDT has, however, recently arrived at the result that this explanation is insufficient. I have earlier suggested that the iron of hemoprotein functions as a catalyst in the nitrogen fixation. N_2 being combined with iron the linkages between nitrogen atoms are weakened and nitrogen is activated.

Leghemoglobin appears in the effective nodules two or three days after the nodules are formed. In the root nodules of peas the rod-shaped bacteria change at the same time to bacteroids. As the fixation of nitrogen ceases when the flowering of pea comes to an end, leghemoglobin changes to green pigment, which we have called legchologlobin. Also, the red nodules of vigorously growing peas can rapidly turn green, within 2-3 days, if the culture pot is transferred into a dark room or the plants growing in light are darkened. Nitrogen fixation then comes to a standstill.

The green pigment contains still an iron atom in its pigment group but a porphin ring is probably not present in it. The transformation of leghemoglobin to green pigment takes evidently place via opening of the porphin ring at the oxidation of a methine group. The absorption spectrum of the pigment and the easy formation of biliverdin from the pigment speak in favour of this concept. Legchologlobin is thus an intermediate product between hemoglobin and bile pigments. It is of special interest that while the nodules are turned green bacteroids disappear and the rods become dominant.

The question how and in which form the nitrogen fixed in the nodules comes to the use of the host plant, is also one of the central questions of symbiosis. Two decades ago it was generally presumed that bacteria build up their cell protein from the fixed nitrogen. Not until in the autolysis of the bacterial cells in the nodules would nitrogen compounds arise—in the first place perhaps ammonium—which can be used by the host plant for its nitrogen nutrition. Should this be the case, nitrogen fixation would be associated with the growth of bacteria, and multiplication and decomposi-

tion ought to take place at a great speed in the nodules. But obviously this is not so.

During nitrogen fixation the root nodules of pea contain, as mentioned, chiefly bacteroids which according to ALMON are unable to multiply. As early as in the beginning 1930's, after we had discovered that amino acids, principally aspartic acid, appear in the growth medium of pea at a young stage, I supposed them to be primary compounds formed in the nitrogen fixation and by no means products of protein breakdown. At the same time I introduced the idea that the host plant receives, via excretion, the same amino acids from the bacteroids in the nodules as are excreted into the growth medium. I considered it plausible that nitrogen fixation takes place on the surface of the bacteroids and that after the formation of the active bacterial mass the fixation is not associated with the multiplication of bacteria. The process occurs with "ready bacterial mass" like, for instance, in the fermentation experiments when bacterial mass is added to a sugar solution. Synthesis of proteins evidently takes place in some measure in the bacteroids during nitrogen fixation but the major part of the fixed nitrogen comes as primary amino acids to the use of the host plant. In fact, BOND showed in soya bean that 'of the nitrogen fixed by the bacteria in nodules a very high proportion probably in the region of 80-90 %, is regularly liberated without appreciable delay into the host cytoplasm.'

I shall now discuss an experiment, made by my collaborators, in which nitrogen fixation and increase of nitrogen in the host plant and root nodules was observed throughout the different stages of growth. During the most intense nitrogen fixation about 90 % or more of the fixed nitrogen passed regularly to the host. No such changes were observed in the nodules that would give rise to the assumption that bacteroids are rapidly formed and decomposed in the nodules.

Formation and function of the root nodules are according to earlier information largely dependent on the quantity of the nitrogen

compounds present in the growth medium and suitable for the nitrogen nutrition of the plant. Moderate quantities of combined nitrogen do not altogether suppress the formation of nodules but according to THORNTON and NICOL greatly reduce the volume of bacterial tissue. The Wisconsin group (FRED, WILSON et al.) has focused special attention in this connection on the carbohydrate level of the host plant and particularly on the relation of carbohydrates to nitrogen. The hypothesis that combined nitrogen reduces the sugar level in the sap of the host plant has gained experimental support by the research of ORCUTT and WILSON who regarded just this fact as inhibitory to nodulation and, hence, to nitrogen fixation. We have examined this question more closely in the sterile culture system and have found that ammonium nitrogen prevents fixation of nitrogen much less than nitrate. In a nutrient solution containing 100 mg ammonium nitrogen, peas still produce large reddish nodules and nitrogen fixation is considerable although the plant with its roots takes up ammonium nitrogen liberally. A quantity of 50 mg nitrate nitrogen in a litre of nutrient solution prevents completely nitrogen fixation although a few small nodules still are formed and they may contain even some red pigment. 25 mg nitrate nitrogen in a litre also stops nitrogen fixation in most cases. The carbohydrate nitrogen ratio in the plants cannot give an explanation to these observations as the pea takes up ammonium more rapidly than nitrates from the nutrient solution. Nitrate has evidently a specific inhibitory effect on nodulation, for instance, in that the nitrite arising from nitrate forms a NO-compound with leg-hemoglobin. This concept is supported by the finding that when we use the branched tube culture system in which the roots are divided into two culture flasks, one branch receiving nitrate and the other being inoculated, beautiful reddish nodules were formed on the roots in the latter. In spite of the fact that the plant in this system takes up with one part of its roots plenty of nitrate, nitro-

gen fixation takes place in the nodules of the other part.

In conclusion, I should like to summarize my concept of the mechanism of nitrogen fixation.

The anaerobic nitrogen fixation by *Clostridium* is very probably a purely reductive process leading directly to ammonia. The first step in the aerobic nitrogen fixation both by *Azotobacter* and leguminous root nodules may, again, be oxidative. After formation of nitrogen oxide (N_2O or NO ?) the oxidation product is reduced following the same path as nitrate reduction.

The idea outlined above is in the first place supported by the following observations: firstly, oxime nitrogen is formed in the aerobic nitrogen fixation but not in the anaerobic one, and secondly, gaseous hydrogen prevents aerobic but not anaerobic nitrogen fixation. Likewise, in the nitrogen fixation taking place in the ultrasonic field where the reaction is for certain oxidative, hydrogen prevents nitrogen fixation; accordingly, hydrogen and nitrogen compete for oxygen. This competition may also explain the inhibitive effect of hydrogen in the aerobic biological nitrogen fixation.

O. N. ALLEN and E. K. ALLEN (Madison, Wis.)

The Production of Rootlets from Nodules of Certain Woody Leguminous Plants

During the course of experiments dealing with the symbiotic association of certain woody leguminous plants and the root nodule bacteria (rhizobia), the attention of the writers was attracted to the origin of rootlets from mature nodules on plants approximately one year old. This report presents briefly the results of detailed histological studies of these nodules found on *Sesbania grandiflora* (a semitropical tree) and *Caragana arborescens* (a shrub). The nodules on these plants tend to be perennial.

All plants were grown from surface-sterilized seed in sterile, nitrogen-free, white quartz sand under greenhouse conditions. Pure cul-

tures of effective rhizobia were added to the seed as inocula. The plants were watered as often as necessary with sterile distilled water and a mineral salt nutrient solution (lacking nitrogen).

On *S. grandiflora* the rootlet-bearing nodules tended to be large, multilobed, and randomly distributed along the tap root. Rootlets always arose within the endodermis of the vascular bundles, emerged at right angles to the vascular strand from which they were derived, and digested their way outwardly through the nodule cortex. Certain rootlets attained a length of 1.5 cm and bore typical root hairs and caps. The hypothesis is advanced here that rootlet origin within these nodules resulted from a stimulation, or irritation, of the host cells caused by the accumulation of byproducts, or growth-promoting substances, produced by the rhizobia in the bacteroid area.

Nodules on the *Caragana* sp. are commonly perennial and lobed in sequence simulating pearls on a string. The terminal lobe is usually the only one functioning in the nitrogen fixing process at any one time, as evidenced by the presence of leghemoglobin and a normally appearing bacteroid area. The rootlets emerged from nodules of this species either (a) in the region of the apical tips as direct extensions of the main vascular strands, or (b) from the sides of the nodule as direct outgrowths of one of the dichotomous vascular branches of an inactive lobe. On this species, in contrast to *S. grandiflora*, nodule rootlets were observed only when meristematic activity of the nodules had ceased. Evidence is lacking at this time that rootlet development from these nodules is related to the properties of the bacteroid area.

H. L. JENSEN (Lyngby)

Nitrification of Pyruvic Acid Oxime by Heterotrophic Bacteria

QUASTEL and co-workers (1, 2) have recently shown that pyruvic acid oxime is readily nitrified in soil, and that its oxidation to nitrite is probably due to heterotrophic organisms.

In agreement with this it was observed [JENSEN (3)] that pure cultures of *Nitrosomonas* do not nitrify pyruvic acid oxime, and a search for oxime-decomposing organisms was made. Three types of bacteria were isolated from soil and found able to produce nitrite from oxime, viz., 1) *Nocardia corallina* which appeared to be the most prevalent and active type, 2) *Alcaligenes* sp., and 3) *Agrobacterium* sp., closely related to *Agr. radiobacter*.

Rapid nitrite formation took place in a synthetic medium containing pyruvic acid oxime (prepared from hydroxylamine-hydrochloride and three to six equivalents of sodium pyruvate) as the only source of nitrogen. Up to 55 % of the oxime-nitrogen could be converted into nitrite within 5 to 12 days, depending on the amount of excess pyruvate present. Glucose inhibited the nitrite accumulation by enabling the bacteria to assimilate the nitrogen as cell substance. Generally some 70 to 90 % of the oxime-nitrogen could be recovered as nitrite plus cell nitrogen.

Nocardia corallina nitrified oxime very vigorously in peptone solution where the conversion into nitrite was almost quantitative within 3 to 7 days. Example:

Incubation hours (25° C)	24	48	72	96
Per cent oxime-N nitrified	0.1	6	52	91

Acetoxime was nitrified to a very slight extent only. Free hydroxylamine was strongly toxic and did not seem to be nitrifiable in sub-toxic concentration. Ammonium sulphate, asparagine and alanine were not nitrified. A number of stock cultures, with the possible exception of *Corynebacterium equi*, did not nitrify pyruvic acid oxime.

ENDRES (4) and VIRTANEN and co-workers (5, 6) have shown that oxime compounds may arise in certain microbial processes, and not only through reduction of nitrate to hydroxylamine as observed by BLOM (7). It is therefore possible to agree with QUASTEL and SCHOLEFIELD (2) that nitrification under natu-

ral conditions may not be the exclusive work of autotrophic bacteria (*Nitrosomonas* and *Nitrobacter*). On the other hand it may be doubted whether the concentration of oxime-nitrogen in natural substrates ever becomes so high that the heterotrophic nitrification will assume considerable proportions in comparison with the autotrophic process *via* ammonia. In any case it appears that only *Nitrobacter* can accomplish the second stage of the whole process of nitrification—the oxidation of nitrite to nitrate.

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GÖSTA FÄHRÉUS (Uppsala)

Growth and Excretion of Phenoloxidase from the Mycelium of Polyporus versicolor

Like other lignin-decomposing fungi, *Polyporus versicolor* forms great amounts of phenoloxidase. This is easily demonstrated by growing mycelium on malt agar plates containing phenols according to the method of BAVENDAMM (1928). It was shown by the author (1949) that not only phenols but also aromatic amines are readily oxidized indicating that the active enzyme is laccase.

The enzyme is freely released from the mycelium into the agar and also into a malt extract solution, if *P. versicolor* is cultivated in liquid medium. However, when cultured in a synthetic medium with glucose, sodium acetate and inorganic nitrogen, growth is almost as equally good as in a malt extract solution, but the phenoloxidase is not released into the

medium until the glucose is consumed and the mycelium undergoes an autolysis. Then the amount of phenoloxidase will be much higher in this solution than in malt extract. These results will be discussed and diagrams showing mycelial growth, phenoloxidase content, etc., will be demonstrated.

The excretion of phenoloxidase in a synthetic medium is slightly increased by substituting an organic source of nitrogen (asparagine) for the ammonium salt. Larger amounts of phenoloxidase will, however, be released from the mycelium on addition of a phenol or aromatic amine to the growing mycelium. This addition will also stimulate the growth and give a higher final mycelial weight.

It is believed that the decomposition of lignin in nature proceeds via intermediate phenolic compounds. These may partly be further used as sources of carbon by the lignin-decomposing fungi, partly, however, they are oxidized to quinones which in their turn may combine with other substances to form part of the humus in soil. Recent investigations in various countries indicate a combination of phenols and amino acids by means of phenol-oxidases. This would account for some of the nitrogen in humus.

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FAUSTO LONA (Milano)

Untersuchungen über Blühbedingungen in Kurztagpflanzen

Neueste dargestellte Befunde vom Verf. ergeben, dass ziemlich alte vegetative Individuen (im Langtag präkultiviert) von ausgeprägten Kurztagpflanzen (wie *Chenopodium amaranticolor* und *Perilla ocymoides*) wenn in Dauerdunkel gebracht zur Blütenbildung kamen. Es ist bemerkenswert, dass in diesen Bedingungen auch solche Objekte den Blühzustand erreichen können, die im Kurztag (innerhalb

24-St.-Zyklen) zwei oder mehr Licht/Dunkel Wechsel für die Induktion erfordern.

Dies ist nicht so ausserordentlich, wenn man bedenkt, dass die photoperiodischen Merkmale bedeutende quantitative Veränderungen—mit Bezug auf das zunehmende Alter und Reifwerden des Individuums—aufweisen; und insbesondere, wenn man sich die fortschreitende Verringerung der photophylen Notwendigkeiten vergegenwärtigt.

Gewissermassen können wir die Möglich-

keit der Blütenbildung in Dauerdunkel als äusserste Vertiefung des unteren kritischen Punktes bis zur Vernichtung des periodischen Lichtbedürfnisses betrachten.

Für die Erklärung dieser Erscheinungen sind noch mehrere Fragen experimentell zu durchforschen; vor allem die Rolle (als Primärfaktor) des Reservematerials, welches sich mit zunehmender Reife der Pflanze anhäuft. In diesem Sinne sind andere dargestellte Versuche bedeutungsvoll.

SESSION 5

Jointly with Section PHF: July 17th, 2—6 p. m., See page 705

SESSION 6

July 18th, 9 a. m. — noon, Attendance: 50 members

Chairman: F. R. HORNE, Recorder: E. ÅKERBERG

SUBJECT:

Sociological Questions in Cultivated Plants

R. O. WHYTE (Walsingham, Norfolk) *The Physiological Nature of a Herbage Plant*

It is generally useful at Congresses such as this to attempt to assess the progress of research in recent years, and to indicate possible fruitful lines of approach for the future. In a section such as ours, dealing with "Agronomic Botany," we have an opportunity on the one hand of reviewing the work of the pure botanists, the physiologists and crop ecologists, with a practical eye. On the other hand, we can review the problems of the agronomist, the husbandman of crops and grasslands, and indicate to the pure botanist, in his laboratory or experimental garden, to what extent his research has been or is likely to be of value in solving them.

I take the humble herbage plant as the key

to this review, because I believe it is for many reasons the most suitable. Certainly no other group of plants is of greater economic importance in Great Britain at the present day. They play a leading rôle in the drive for increased agricultural production, and at the same time they receive the most murderous treatment by the grazing animal, or by man with his scythe and cutter-bar, intent on conservation in the form of hay, silage or dried green crops.

Every time the grass or clover plant produces the leaves which are part of its normal processes of growth and ultimately of reproduction, along comes agronomic man with his recently acquired standards of good pasture husbandry, and the patient herbage plant is back where it started. No other plant suffers so much. The wheat and the soja bean are granted the honour of continuing their normal

life history through to fruiting, to the production of seed. The vegetative cabbage and lettuce are permitted to form their hearts and then death is sudden. But the perennial herbage plant has to go on suffering year in year out, always growing up hopefully and strongly under the influence of artificial stimulants, always going back to the beginning.

And yet our humble herbage plant is expected to do all manner of things. It is expected to produce nutritive green food which the grazing animal can utilize for as much of the year as possible, through summer droughts and winter storms and frosts. It is expected to produce heavy crops of green herbage for conservation under close and repeated cutting. The green or conserved fodder is confidently expected to be rich in proteins, starch equivalent, vitamins, hormones and the unknown quantities upon which so many graziers rely. And at the same time, the roots of these herbage plants from which the tops are repeatedly removed are expected to influence soil structure and to improve the organic matter status of the soil, while the tops themselves are fully expected to conserve and protect the soil against the erosive action of wind and water.

Those who work with herbage plants certainly work with wonder plants!

Some of the problems being studied by the plant physiologists are of great importance to those who breed, manage and utilize herbage plants. Probably the most important branch of plant physiology is the study of plants in relation to the environment in which they grow wild, or in which they are cultivated. These studies vary from the analytical breakdown in laboratory trials of the total environment into its various parts to the more geographical studies of the behaviour of herbage plants at different points within the latitudinal range of adaptation. From them come not only valuable data on reactions to light and temperature, but also some indication of the relation between environment of different latitudes and altitudes and growth forms or eco-

types so important in the breeding or selection of strains for economic use as hay or pasture plants. Some of the pasture types recognized by British breeders have been produced in semi-natural conditions, such as prevail in the Leicestershire fattening pastures, from which Professor T. J. JENKIN collected some of his original types. The controlling ecological factor here is the biotic one of the grazing animal.

Other vegetative ecotypes in outward appearance similar to the pasture types may obtain their non-reproductive characteristics because the environment in which they find themselves is only partially conducive to reproduction. There is a very great difference between the fully reproductive stemmy types of cocksfoot found by Mr. L. J. S. LITTLEJOHN and myself in the dry hillsides of Cyprus, and the 100 per cent vegetative selections from Oron cocksfoot which I saw in the breeding grounds of Professor ROBERT WEIR at Ontario Agricultural College.

I would like to see tillers or clones of the Ontario material distributed among agronomic botanists throughout the entire range of latitude and altitude in which the species could grow, just to see how the type would behave. It would be interesting to know if the Ontario environment is such that these plants are prevented from expressing their genetical constitution to the full, and to discover what the effect of other environments might be on the reproductive behaviour and growth forms of the type. I believe that some plants of Oron cocksfoot have been grown at the Grassland Research Station at Stratford-on-Avon, and have produced seed. Information of this type would be of some value in the theoretical location of seed-producing areas of vegetative or pasture types, the seed obtained to be sown for pasture use in a different environment.

The results obtained some years ago after the transference of seed of pasture strains from Wales to Australia, and the observations made by New Zealand agronomists to the effect that their strains never seem quite to

equal their New Zealand performances when tested elsewhere would appear to suggest a further fertile field of research. It would be interesting to have crosses made at one or more breeding centres at different latitudes, and then to distribute the F_1 generation seed again throughout the latitudinal range of the species being studied. I believe a carefully coordinated scheme of experiments might produce some very interesting data on the genetic constitution of herbage plants and its stability, or capacity to express itself under the influence of different environments.

In all work on growth forms in relation to reproductive capacity in herbage plants, it is essential to know the marks of identification of a vegetative or reproductive plant. More information on the date of formation of flower primordia would be of considerable practical agronomic value in the management of pastures and seed stands of herbage plants. The few studies which have already been made on flower primordia in grasses have been most interesting and promising and should of course be the basis of all studies of the growth and reproductive behaviour of herbage plants. Even flower primordia do not tell the whole story, as it appears that a herbage plant may be in a ripe-to-flower condition at the end of a winter, although the criterion of reproductive primordia might not then be available for identification. The only possible indication of ripeness-to-flower at the moment would appear to be the minimum leaf number put forward for example by Professor F. G. GREGORY and his associates.

Let us now turn from the external manifestations of the change from a vegetative to a reproductive state and the progress of reproduction through its various phases to the internal causes for these changes and progressions. It is inappropriate to attempt to discuss here the experimental evidence and theoretical interpretations which have been produced relative to the "flower hormone." This was discussed fully by Prof. GREGORY at the Symposium held by the Society for Ex-

perimental Biology at Oxford in 1947, on growth in relation to differentiation and morphogenesis.

The agronomic botanist concerned with herbage plants cannot fail to wonder at the remarkably small effect which repeated removal of functional leaves and damage to tender growing points carrying the primordia has on the physiological behaviour of the plant and its ultimate progress towards reproduction.

As no-one has yet isolated the flowering hormone and as the whole picture is, therefore, still speculative, a little more speculation may not go amiss at this point.

Is there any connexion between total content and movement of hormones within a plant and the annual, biennial or perennial habit? Might it not be that, when an annual or biennial goes to seed, all the hormone in that plant is removed in the seed, and none remains to revive the meristematic activity at the base and so lead to the formation of new tillers? Might it not be that, in a perennial plant, only part of the hormonal content of a plant goes off with the seed head and stalk, and enough remains at the base to meet the needs of new tiller growth. And the higher the amount or the concentration which remains, the more active the new tillering.

The agronomist is coming more and more to realize the superiority of maiden (first-year) leys, and of spring grass over autumn grass. The agronomic botanist might explain those practical observations on the basis of seasonal behaviour in relation to reproduction. The maiden ley is much younger physiologically and more active towards reproduction than the older ley, which probably has a much higher proportion of vegetative tillers in which the reproductive or flower hormone has not been elaborated. Also a cocksfoot/white clover ley in spring and autumn may appear to be identical in growth stage and suitability for grazing and cutting, but would the plant physiologist agree?

There is an interesting parallelism between the research of the plant physiologists, and

that of the animal physiologists on the animal sex hormone content of the plants. The pioneer work on this subject is being done by Dr. S. BARTLETT and his colleagues at the National Institute for Research in Dairying at Reading. The rôle of these substances in plants has not yet been fully explained, but that they may affect the reproductive system of the grazing animal and cause infertility has been demonstrated in Western Australia. The workers at Reading have concentrated more on a study of the occurrence of oestrogens in British grasses and clovers, and have found that considerable activity exists. The potent species are *Lolium perenne* (S. 23), the New Zealand Short Rotation Hybrid ryegrass (H. I.), *Dactylis glomerata* (S. 37), and *Trifolium pratense*. On the other hand *Medicago sativa*, *Trifolium repens* and *Phleum pratense* show little activity.

In each of the potent species, activity has been found in all parts of the plant tested, the leaf, petiole, stem and inflorescence. There is considerable seasonal variation and the various plant organs do not have maximal concentrations at the same time. When chloroplasts are precipitated from the juice obtained by crushing plant material, the bulk of the oestrogen occurs in the precipitate. The Reading workers believe that the high oestrogen concentration in the potent species may be associated with reproduction in the plant. Spring growth of grass, which is associated with high oestrogen concentration, precedes flowering, but when autumn growth takes place the plant is not in a reproductive condition. Broad red clover, on the other hand, which has repeated high concentrations of oestrogen, will produce flowers throughout the summer and autumn.

The agronomists and biochemists on my staff are collaborating in a further extension of this work, by growing pure stands of S. 23 and H. I. ryegrass and of Broad Red clover, for drying artificially in 1951, to be compounded into balanced cattle cakes for feeding to dairy cattle in the winter of 1951/52. Thus

artificially dried material of known oestrogen potency will be used in a properly conducted feeding trial, a good example of collaboration between the agronomic botanist and the specialist in animal nutrition.

These then are some of the lines on which I consider the agronomic botany of herbage plants might be expected to advance in the coming years. There is great scope for academic and practical research, and we can only pray for the peace under which collaboration between scientists of many nations shall be possible.

Discussion

OLOF SVANBERG: As regards the total content and movement of hormones etc. in the herbage plants, a number of earlier well known substances may exert the same effect on grazing animals. Thus the spring grass contains much less lignin than the autumn grass, the spring grass may contain 10–19 per cent of sugar against 2–4 p.c. in the autumn grass. Autumn grass, not eaten by sheep, with a low sugar content, may be eaten by the same animals "to the roots" after being frozen, when the sugar content is higher. The phosphorus content may also interact, being as a rule higher in the spring grass, which in co-operation with the sugar gives rise to a more favourable condition in the rumen.

The hormones of the plants are very interesting, but one must not forget the old substances for the new ones.

GWILYM EVANS: I have found that *Oron* cocksfoot appears to produce seed in a normal manner at Aberystwyth. This may be due to the fact that *Oron* has been partly synthesised with plants selected from a pasture strain of cocksfoot bred at Aberystwyth.

L. HEDIN (Rouen) *Recherches sur l'écologie des prairies françaises: Un essai de classification*

L'intérêt des efforts des botanistes est incontestable, mais il est essentiellement descrip-

tif. Dans l'étude de la succession des groupements végétaux, ils se contentent généralement d'indiquer le sens de l'évolution de la végétation, tel qu'il résulte de leurs observations. La nécessité de connaître les conditions culturelles de cette évolution fait apparaître les besoins d'une étude expérimentale des associations prairiales. La révision des concepts traditionnels de la phytosociologie a conduit les pastoralistes et au premier lieu le Dr. WILLIAM DAVIES à dégager la notion d'«agro-climax prairial» qui peut se définir comme le stade d'amélioration culturale maximum qu'il est possible d'atteindre à partir d'un type médiocre de prairie donnée. Le Dr. WILLIAM DAVIES a montré, pour l'Angleterre et le pays de Galles, l'importance de deux séries dont les climax sont la prairie à ray-grass-trèfle blanc et l'Agrostidaie.

Reprenant les vues du grand pastoraliste anglais pour ce pays infiniment varié qu'est la France, L. HEDIN retrouve une sériation analogue dont voici le schéma pour les principaux types de prairie de notre pays.

Série de la prairie à ray-grass-trèfle blanc

a) *Prairie paturée* — Le Lolietum doit être considéré comme l'agro-climax prairial des prairies des plaines et basses collines de la zone atlantique partout où le sol est bien pourvu en colloïdes argilo-humiques et en chaux.

b) *Prairie fauchée* — Dans le Nord-Ouest les exigences écologiques de l'Arrhénateraie coïncident à peu près avec le Lolietum, mais il est incontestable que dans une grande partie de la France le Fromental (*Avena elatior*) végété dans des sols plus secs, moins riches en chaux (Arrhénateraie siliceuse) et à une limite altitudinale plus élevée.

L'Arrhénateraie est le terme d'évolution de la Moliniaie alcaline, du Brometum fumé, de la Holçaie.

Série de l'Agrostidaie

a) Agrostidaie des sols filtrants de la zone atlantique.

b) Agrostidaie montagnarde, qui atteint son optimum écologique entre 800 et 1000 mètres.

La prairie à *Trisetum flavescens* semble être l'intermédiaire entre l'Agrostidaie et l'Arrhénateraie, entre 800 et 2000 mètres (altitude limite).

Pelouses méditerranéennes

Après les cultures, avant l'envahissement du sol par *Brachypodium phoenicoides*, le stade à *Cynodon Dactylon* et *Dactylis glomerata* correspond au meilleur rendement fourrager.

Discussion

OLOF SVANBERG: Il n'est pas nécessaire d'exprimer le grand intérêt des travaux très modernes de Mr. HEDIN.

Nous avons reçu, l'année dernière, de nombreuses publications françaises traitant du sujet «phosphore et vie», et nous avons pu constater la nécessité impérieuse de fumer les prairies françaises avec des engrais phosphoriques pour obtenir une production laitière satisfaisante et pour maintenir les bestiaux en bonnes conditions pour les grands rendements.

Nous avons en Suède les mêmes problèmes. Aujourd'hui, dans un grand nombre d'exploitations, on a effectué par les engrais de grandes améliorations des prairies et, de ce fait, la production laitière a effectué de grands progrès.

Après avoir perfectionné les prairies de cette manière, on peut observer que leurs compositions botaniques ont été profondément transformées. L'aire prairiale, par exemple, peut être complètement envahie par d'autres graminées, les trèfles peuvent pousser d'une manière florissante, etc. . . .

Il est certainement exagéré de prétendre que le terrain soit tout et les semences rien. S'il est nécessaire d'avoir une description de la végétation actuelle, il est intéressant aussi de savoir comment elle peut se transformer sous l'influence d'engrais différents.

R. DE VILMORIN: La question exposée par Mr. HEDIN est intimement liée à celle des écotypes de graminées dont l'étude est fort impor-

tante pour la constitution ou reconstitution des prairies à faucher. L'expérience montre que, sous les climats très variés de la France, il existe pour chaque espèce de graminée, un grand nombre d'écotypes différents par des caractères physiques et physiologiques très appréciables et constants. Le problème se pose donc de la production à l'état pure des graines de graminées destinées aux mélanges adaptés aux diverses conditions écologiques. Nous nous en occupons très activement en France. Il serait précieux de connaître le point de vue de tous les chercheurs et agronomes s'intéressant à ces questions et aussi d'étendre les échanges d'écotypes sur le plan international.

L. HEDIN: L'Agriculture française s'efforce d'utiliser les phosphates naturels d'Afrique du Nord, qui dans certaines conditions ont donné de bons résultats, comparables à ceux obtenus par l'emploi des scories.

La littérature agricole française indique depuis longtemps l'existence des antagonismes: notamment entre *Fagopyrum esculentum* et *Spergula arvensis*. Les Anglo-Saxons (Dr. WILLIAM DAVIES) contre-indiquent le semis de *Lolium perenne* et de *Festuca pratensis*. Le professeur L. GUYOT de l'École d'Agriculture de Grignon poursuit actuellement des recherches tendant à prouver le caractère réel de l'association végétale. Il a reconnu, en plus de *Calamagrostis epigeios*, la toxicité des racines de *Hieracium pilosella*, *Thymus vulgaris*.

HUGO OSVALD (Uppsala)

On Antagonism between Plants

In the autumn of 1945 rape (*Brassica napus* L. f. *oleifera* Metzg. and *B. rapa* L. f. *oleifera* Metzg.) was sown on one of the fields of the experimental area of the Plant Husbandry Institute of the Royal Agricultural College at Ultuna. Although the field had been cultivated several times, there were still patches with queck grass (or couch grass) (*Agropyron repens* PB.). It was observed that on these patches

the rape germinated and developed very poorly as compared with the rape on other parts of the field. Since the soil is fertile and the crop had been supplied with a fair amount of fertilizers, it was hardly possible to explain the difference in development as a result of root competition about nutrients. The poor growth of the rape seemed to be caused by some other factor. It was close at hand to think of excretions from the *Agropyron* roots, i. e. root exudates.

The observation recalled to my mind some observations I had made when working with other problems many years ago—observations which had never been explained satisfactorily.

As a botanist at the Swedish Peat Reclamation Society I had had to study the vegetation of leys sown with grasses in pure stands and with different clover and grass mixtures. Several times it had struck me that some grasses, for instance red fescue (*Festuca rubra* L.), kept rather free from admixtures of other grasses and weeds, while the plots of other grasses, for instance of timothy (*Phleum pratense* L.), after a few years were badly infested with other species, mainly weeds. Now, in the case of red fescue the dense growth of this species might provide a fairly good explanation for the lack of weeds. But on the other hand, it was difficult to explain why weeds had not invaded the plots before the fescue had become so dense and vigorous. And, moreover, it was not possible to explain in this way why meadow oats (*Arrhenatherum elatius* M. & K.), which generally form a rather light and open stand, could keep free from weeds. Further, why did clover sown together with cocksfoot (orchard grass) (*Dactylis glomerata* L.) disappear much faster than clover sown together with timothy?

At the time when these observations were made, I never got an opportunity to look into these problems. One of the reasons was perhaps that the so-called toxin theory, presented by a number of scientists at the Bureau of Soils in U. S. A. in the beginning of the twentieth century, had never been accepted. According to this theory certain unproductive soils con-

tained toxic substances, which prevented or retarded the growth of many plants. As a matter of fact, DE CANDOLLE in 1832, had presented a theory of antagonism between phanerogams. But it did not seem promising to try to tackle the problem along these lines.

However, I could never quite get rid of the problem of competition between clover and grasses, and I was rather strongly reminded of the problem when, in 1927, I visited Dr. HARTWELL, Kingston, R. I., U. S. A., and saw his experiments on the influence of certain cultivated plants upon subsequent crops. In recent years, and particularly through the discovery of the biological effects of antibiotics and phytohormones, the question of growth inhibition caused by extremely small quantities of substances produced by plants has attracted revived interest. If hormone derivatives in such small quantities as, say, 10 mg/sq. meter could exercise a marked effect on many plants, it seemed quite reasonable to me that extremely small quantities of root exudates might also have an influence upon plant growth and in the competition between plants. The observations on the rape field in 1945 therefore gave the impetus to start an investigation on this problem.

Before describing my experiments I should like to emphasize that this problem is a rather complicated one, and although it has received considerable attention, very conflicting conclusions have been drawn. A detailed review of the subject was given by LOCHWING in 1937. He came to the conclusion that "there is no evidence of the presence of soluble toxics in normally aerated soils sufficiently supplied with plant foods and calcium carbonate — — — there is no evidence of plant excretions conferring toxic properties on the soil."

The investigations I started aimed in the first place at discovering whether the roots and stolons of *Agropyron* might contain any substance with detrimental or retarding effects on the germination and development of rape. Later, the scope of the investigations has been widened to involve the whole question of the

biological effect of root exudates and the rôle of these substances within agriculture and plant ecology.

The first experiments were made in the following way. Stolons and roots of *Agropyron* were dried and ground, and extracts were prepared with different solvents: weak ammonia solution, alcohol, and acetone. Subsequently, different concentrations of the extracts were used in germination experiments with seeds of rape in Petri dishes, later also with oats.

It was proved by the experiments that the extracts in very low concentrations had a stimulating, but in higher concentrations a strongly retarding or detrimental effect on the germination of rape and oats seeds, and that there were obvious differences between different organisms in their sensitivity to the toxic substance. Together with the observations on the rape field these results seemed to justify the conclusion that the great competitive ability of the queck grass was due, at least partly, to the effect of its root exudates (OSVALD 1947).

At a meeting of the British Ecological Society in 1946, I read a paper on these investigations. In the following discussion it was argued, for good reasons, that the experiments did not prove that the active substance was an exudate, it might just as well be some other chemical substance which had been extracted from the roots and stolons. In subsequent years, I have therefore tried to demonstrate the effect by other methods.

At a visit to Skarvik just outside Gothenburg I happened to get across a red-fescue meadow with an extremely dense and vigorous growth of this grass and without any admixtures at all of other plants. A sample of the soil from this meadow was extracted, and it was found that the extract had a strongly detrimental effect on germination of rape and some other plants, while no such effect at all was obtained with soil extracts from cultivated arable land. It seems probable that the properties of the Skarvik soil were due to exudates from the red fescue, and, if so, this would support the conclusion that the ability of red fescue to form pure stands

and keep other plants away would be partly due to the effect of its root exudates. There was, however, the possibility that the soil might have contained a substance not affecting the red fescue but toxic to other plants.

In another series of experiments some grasses were sown on filter paper and allowed to grow for three weeks. During this time most of them developed a dense root felt. The plants (with the roots) were then removed, and the filter paper was used for germination experiments with rape seeds in Petri dishes. It was found that there was little or no effect on the percentage of germination, but in some cases a very obvious effect on the development of the roots of the rape seedlings. This effect could hardly be caused by any other factor than exudates absorbed by the filter paper. On filter paper with exudates from oats, barley, and perennial ryegrass the rape seedlings had strongly abnormal roots. On filter paper with exudates from red fescue the roots were less abnormal. The strong effect of oats and barley may be due to the fact that these species had developed a much larger quantity of roots than the other grasses and probably also had produced larger quantities of exudates (OSVALD 1949).

Since no significant differences in germination percentages were obtained by this method, as was also later emphasized by Dr. G. WILSON working at my institute and repeating the experiments, it seemed necessary to design a method by which the root exudates could be collected. Professor HOLGER ERDTMAN, Stockholm, with whom I discussed the problem, suggested the method employed by TODD and his collaborators in a comprehensive and successful study of the root exudates of tomato, their chemical structure, and their effect on cysts of potato eelworm. Instead of using, as TODD et al., an ordinary soil for growing the exuding species, I preferred to use sterile quartz sand. After a small preliminary test, which proved that a solution with retarding effect on germination was obtained by this method, the experiments are now in progress on a fairly large scale. In slightly sloping vessels of stainless

steel with an area of about 0.25 m² and a depth of 7 cm, and with an outlet in the lower end, different plants are grown and watered with distilled water or nutrient solutions. The runoff from the vessels is collected in glass flasks. The solution thus obtained is concentrated and used for germination experiments with different species.

In the first experiments rye has been used as the exuding plant, and wild oats (*Avena fatua* L.) as the test plant. These two plants were selected for the following reason. In a study of old Swedish agricultural literature I had found that during the eighteenth century it was recommended to the farmers to grow rye, when the wild oats had become too frequent in the fields. Rye will kill the wild oats, it was claimed. This statement was undoubtedly founded on long experience, and it seemed to be of interest to test the reliability of the statement. It should perhaps be mentioned that in the first experiment *Cucurbita* was employed as a test plant, mainly because this species had proved to be very sensitive to growth regulating substances. This species, however, did not respond at all to the rye exudates. The seeds germinated just as well on the exudates as on distilled water. After this rather disappointing result the wild oats (and red fescue) were used as a test plant. So far only a few preliminary experiments have been completed. But the results are rather interesting. In one experiment the germination percentage of wild oats was 10 per cent lower on exudates from rye than on distilled water, while exudates from wheat and barley did not exercise any such influence. In another experiment the exudates from red fescue lowered the germination percentage of wild oats with 10–20 per cent. More obvious than the depressing effect on the germination percentage was the influence of the exudates on the development of the wild oats seedlings. Although most of the seeds germinated, the subsequent growth of the seedlings was strongly retarded or practically inhibited. This is clearly demonstrated by some of the Petri dishes from one of the experiments. Consequently, the

results from these experiments seem to be in good agreement with the recommendations in the eighteenth century.

TODD and his collaborators have shown that root exudates from tomato have a very marked physiological effect, namely, on the hatching of potato eelworm cysts. In 1948 GRAY and BONNER found that the leaves of *Encelia farinosa* exude a substance which exerts a detrimental effect on the growth of surrounding plants. The preliminary experiments now mentioned seem to justify the conclusion that root exudates may also have an effect upon the germination of seeds and on the development of the seedlings. This effect may sometimes be stimulating, sometimes retarding, if not killing. It seems probable that the root exudates play an important rôle in the competition between plants, in cultivated fields as well as in natural vegetation.

The competition between plants in cultivated fields mainly applies to the competition between cultivated plants and weeds and to the compatibility of different ley plants. The question of competition between cultivated plants and weeds has received much attention in recent years. The incompatibility of rye and wild oats has already been emphasized. The relationships between potato and queck grass seem to be similar. On the other hand some weed species seem to be favoured by certain cultivated plants. This seems to be the case with *Chenopodium album* in potato crops, and with *Agrostemma githago* and *Viola tricolor* in rye crops.

With regard to the compatibility of ley plants a few cases have already been mentioned in the beginning of this paper and it may not be necessary to mention more examples.

In natural vegetation the antagonism between, or the compatibility of, plant species may be of great significance to the grouping of plant species in communities. Only a few examples may be mentioned. LINNAEUS, in his account of his travel to Gotland, mentions that *Allium ursinum* will kill a number of other species, and anyone who has had an opportunity to study *Allium ursinum* will be able to certify

that this species is always growing in dense and practically pure stands. This is in good agreement with an old observation concerning another *Allium* species, i.e. *A. vineale*. A few days ago Dr. HARRY GODWIN told me that when he was a young student of Cambridge, one of his professors told him that British farmers used to say that it was impossible to grow oats successfully in fields which were infested with *A. vineale*. NORDHAGEN in his studies of Norwegian sea-shore vegetation has made a number of statistical field analyses showing, as he has emphasized, that the *Arrhenatherum elatius* community is always very poor in species, although the *Arrhenatherum* belt occurs at a level which is usually very rich in species. This tallies very well with the observations from ley mixtures concerning this species which have already been referred to. SELANDER in his comprehensive study of the mountain vegetation of Lule lappmark in Northern Sweden, referring to my experiments, emphasizes "that a number of rare mountain plants are lacking not only in communities where the plant cover is closed but in very thinly covered meadows and grass heaths as well. The plants most strictly confined to (bare) mineral soil, e.g. *Sagina caespitosa*, *Braya linearis*, *Arenaria humifusa*, *A. norvegica*, *Carex nardina*, *C. glacialis*, most *Drabae*, *Potentilla nivea*, *Arnica alpina*, and *Oxytropis lapponica*, seem able to tolerate the presence of but very few commensals, and of grasses usually none at all.—This can, possibly, be explained from the effect of root exudates of the gramineous plants."

A great number of similar cases could be quoted, but at present these examples may be sufficient.

Since, according to the title, this paper should deal with antagonism between plants, it should finally be added that antagonism is not confined to the effect of root exudates. The biochemical antagonism also embraces the effect of chemical substances from other parts of the plant. The case of *Encelia* has already been mentioned. In other cases rain water that has been in contact with, for instance, yellowing

leaves of certain trees has an obvious effect on the composition of the ground flora.

A great deal of experimental work is required to elucidate the problem of antagonism, or more generally speaking, the degree of compatibility of plants.

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Discussion

E. W. FENTON: I wish to draw your attention to the distribution of *Festuca rubra* and *Festuca ovina* in Scottish Hill grazings and its relation to root exudates.

A similar interrelation exists between *Caluna vulgaris* and *Pteridium aquilinum* in Scottish Hill grazings.

JOAN M. THURSTON: Two questions: 1) Had the *Avena fatua* seeds used in the experiments been treated in any way to overcome their natural dormancy? 2) Does the exudate from *A. fatua* roots antagonise germinating rye?

JOHN L. HARPER: Is it possible that the inhibiting effects which have been observed for rye exudates on the growth of wild oat seedlings are due to high osmotic pressure of

the extracts used? In the experiments which professor OSVALD has shown, there is a heavy precipitation and some crystallisation in the dishes to which extracts have been added but not in the controls. Such an osmotic pressure effect would be comparable to that of fertilizer placement in the root region which may also inhibit growth of cereals.

H. OSVALD: In reply to Miss THURSTON's questions:—1) No, but the seeds germinated quite well in dishes with distilled water.—2) I haven't yet made the reverse experiment.—In reply to Mr. HARPER:—Probably not.

R. F. DAUBENMIRE (Pullman, Wash.) *Contrasted Effects of Different Types of Animals and Seasons of Grazing on the Botanical Composition of Virgin Grassland*

Grazing by sheep and by cattle have different effects on the *Agropyron spicatum*-*Poa secunda* association of eastern Washington. The course of retrogressive succession is complicated by the aggressiveness of the introduced *Bromus tectorum* which has found the climate a close match for its ecologic requirements, and by the fire factor. Under sheep grazing the amount of *Bromus tectorum* can be altered easily by grazing practices, but under cattle grazing this is not true.

Discussion

OLOF SVANBERG: I should like to ask: what was the quality of the pastures in question as to phosphorus, potassium and nitrogen? Did you give some fertilizers in order to maintain the productivity of the pastures or is it more a question of extensive use of the grasslands?

R. F. DAUBENMIRE: Although these grasslands are subject to heavy use, intensive management involving fertilizers has not to my knowledge been attempted.

CHARLES KILLIAN (Alger)

Nouvelles observations sur les conditions édaphiques et les réactions des plantes indicatrices dans des réserves de pâturages de la région alfatière algérienne

J'ai insisté, dans plusieurs de mes publications antérieures, sur le rôle fondamental que jouent les conditions édaphiques dans la répartition des plantes désertiques et subdésertiques de l'Algérie. Une reprise de ces études dans les pâturages mis en défens des Hauts-Plateaux et illustrée par des graphiques où figurent principalement les caractères physiques des sols m'a montré une véritable zonation dans la végétation des bas fonds, irrigués par les crues. Celle-là est en relation très étroite avec les caractères différentiels, chimiques et physiques, de leur substratum.

Nous voyons ainsi juxtaposés des hygrophytes, près des mares d'eau temporaires, avec des peuplements de Légumineuses, occupant en masses denses les bas fonds. Le *Medicago denticulata* qui domine aux stations plus sableuses est remplacé par des gazons de *Cynodon dactylon* sur les sols exondés, plus limoneux et argileux. Il est relayé, à son tour, aux endroits régulièrement exondés, par *Artemisia Herba-alba* dont le substratum plus compact présente un maximum de bonnes qualités, physiques et chimiques. Aussi le semi-nomade le remplace-t-il par des cultures de céréales dont la friche laisse subsister une foule d'espèces adventives.

Dans cette même zone se trouve enclavée une végétation à buissons, représentée par le *Zizyphus Lotus*, qui, par bonne année, atteint un maximum de densité, colonisant, par ses espèces vassales, les terres vierges des alentours; grâce à l'excellente protection que leur offre leur branchage touffu il humifie les sols dont l'amélioration se manifeste, pédologiquement, par une hausse importante de leur fraction dispersée, de leur hygroscopicité et une hausse des fractions humiques.

Au point de vue botanique elle se caractérise par l'augmentation de plantes de grande

taille et l'apparition de Graminées à feuillage tendre et de bonne qualité fourragère. Là s'accumule un maximum de détritus végétal.

Le *Zizyphus Lotus* est donc un colonisateur de premier ordre. Son éradication par la population autochtone entraîne un ravinement du sol, une disparition des herbes tendres, remplacée par des héliophytes de moindre valeur fourragère et, enfin, l'ensablement par ascension, suivi de l'apparition de l'*Aizoon hispanicum*, halophyte, si étrange dans un milieu essentiellement glycyphytique.

Tous ces changements se répercutent en détail sur la composition des cendres des divers végétaux types.

Ils sont caractérisés par leur quotient $\frac{P_2O_5}{CaO}$, trop uniforme cependant, par l'excès du CaO , la somme $N+P+K$ mais surtout par leurs taux azotés et phosphoriques, en progression régulière et le pourcentage des fibres crues, en régression avec leur valeur fourragère.

Discussion

OLOF SVANBERG: Quel pour-cent en matière organique totale ont eu les sols algériens en question?

CH. KILLIAN: The content of carbon can vary between 0 and 3 per cent.

H. R. OPPENHEIMER (Rehovot)

Plant Reactions as Indicators of Irrigation Requirement

Irrigation of agricultural crops in arid regions is to this day often carried out empirically or founded on soil moisture studies. An agrophysiological approach to the problem of economical water use began about 1930 with the studies of MAXIMOV and his school at Saratov and MAGNESS and FURR in the U.S.A. The results since obtained are very encouraging but show that research methods must be adapted to each single crop, and interpretation must be made with due regard to developmental stages, rooting habits, weather conditions, etc.

Growth in height or increase of leaf surface and gain of dry substance can be used for checking irrigation schemes in field crops. The saturation deficit of leaves and the rise of their osmotic value can inform us about the direct effect of water shortage, but their determination is not simple enough for use by farmers. The same is true of transpiration studies.

Useful indicators are growth of fruits and stomatal aperture, both reacting to even slight degrees of water shortage, before wilting sets in. Interpretation of data becomes possible by knowledge of the behaviour of heavily irrigated control plants. LLOYD's alcohol fixation method for the establishment of stomatal width has often been chosen for unsuitable objects, while MOLISCH's simple infiltration method could be successfully adapted, by the author, to citrus and apple trees.

The same method was recently found useful for bananas in the Jordan Valley by SHMUELI who also is developing physiological methods for maize, potatoes etc., while other students in Israel study alfalfa, tomatoes and olives.

Results confirm that for optimum production a plant should never undergo acute water shortage (MAXIMOV) and show that soil moisture should not be allowed to come too near the ultimate wilting percentage.

With citrus trees root suction force has been found decisive for the availability of soil water which obviously does not depend on soil properties alone.

International cooperation for the develop-

ment of this branch of applied botany is recommended.

Discussion

OLOF SVANBERG: I must draw the attention to the fact that the transpiration coefficients (i.e. the kgs of water necessary for the formation of one kg of dry matter) of the plants are very different according to the nutritional level of the plants, a careful use of fertilizers being in favour of the utilisation of available water. Thus different levels of fertilizing must interact and give rise to different critical figures as presented by the author.

GWILYM EVANS: To what degree can applications of nitrogen correct deficiencies in water supply? In Britain nitrogen requirements for seed production of grasses are doubled from west to east as the rainfall is halved.

H. R. OPPENHEIMER admitted that transpiration coefficients indicating specific water requirements of crops are found relatively low, if composition and concentration of the soil solution are optimal, but rise under unfavourable conditions of both nutrient and water supply.

A partial replacement of water as a factor of agricultural production by nitrogen seems hardly imaginable, and the speaker felt unable to offer an explanation for Dr. EVANS' surprising statement. Insufficient dissolution, penetration or partial volatilisation of the nitrogen fertilizers under the drier conditions may possibly be thought of.

SESSION 7

Jointly with Section CXT, EXT, and GEN: July 18th, 1—4 p. m., Attendance: 50 members

Chairman: W. RUDORF, Recorder: A. MÜNTZING

SUBJECT:

Origin and Evolution of Cultivated Plants, Gene-Centre Differentiation and Synthesis

F. G. BRIEGER (São Paulo)
*Distribution and Origin of Maize and the
Theory of Collective Centres of Origin*

Since the time of DARWIN, the study of the origin of domesticated plant or animal species has been used as a means to elaborate or at least to obtain support for current theories on the evolution of species. The justification for this lies clearly in the fact that in these cases evolutionary changes have undoubtedly occurred in a relatively short time and under the directing effect of artificial selection which does not differ essentially from natural selection, being only stronger and less varying in direction. Among cultivated plants, maize occupies in this respect a very special position since here artificial selection has resulted in producing a domesticated form, considered as a good species, *Zea Mays* L., completely unknown as a wild plant.

Time and place of the origin of maize are still to some extent unknown. Recent archeological evidence has shown that forms of maize, essentially alike to the modern types, have occurred long ago in two widely separated locations: around 800 B.C. near Trujillo on the Peruvian coast (CLIFFORD EVANS, BIRD) and around 2000 or 3000 B.C. at Bat Cave in New Mexico (MANGELSDORF and SMITH). If we accept current belief that man did not arrive in the Americas much before 30 000–20 000 B.C., we may estimate that the domestication of maize cannot have started much before 6000 to 5000 B.C. (BRIEGER). With regard to the

place of origin, I think we may be quite justified in accepting an American origin. All documentary evidence, recently reviewed by MANGELSDORF and REEVES, proves that maize was unknown in the Old World before Columbus. ANDERSON has considered the possibility of an origin in south-eastern Asia, but material from Assam (ANDERSON and STONOR, BRIEGER) gives no clear-cut proof to this hypothesis. These Assam races show similarity with races of the Amazon Basin, and also with one race from the Pacific region of north-western Colombia (BRIEGER). There is no reason against assuming that they are derived from a very old, but still post-Columbian dissemination of South American maize.

If we want to narrow down the area, we may first state that all authors agree that the North American area may be left out of consideration. Older hypotheses oscillated in general between two extremes, parting from the idea that the origin of this cereal must be geographically and historically connected with the two regions where the highest level of civilization had been attained in pre-Columbian times, i.e. the Maia-Toltec-Aztec area in Central America and the Chimu-Inca area in the South American Central Andes. This hypothesis is evidently as unfounded as the conclusion that the Roman Empire coincided with the area of the origin of wheat, that of the German Empire with the origin of the potato or that of Brazil with the origin of *Coffea*. Maize which served as the economic basis for these American civilizations was evi-

dently a prerequisite for the development of the latter, and not, vice versa, a consequence of these civilizations.

The actual distribution of indigenous races of maize gives no support to a hypothesis of a Central American origin, and most modern authors leave this possibility out of consideration. MANGELSDORF and BRIEGER agree that the most probable region lies somewhere near the eastern foothills of the Andes. I think, furthermore, one may rule out in the south the region of the big swamps, called in Brazil "Grande Pantanal," and the tropical zone of eastern Colombia and Peru in the north, leaving as probable centre of origin the eastern low-lands of Bolivia and the western parts of Brazil, mainly in the State of Matto Grosso. But new facts may force us to revise these conclusions based so far on indirect evidence.

The study of the geographical distribution of wild relatives of maize does not offer very great help. *Euchlaena mexicana* is limited to a rather narrow area in Mexico and Guatemala. The numerous species of *Tripsacum* cover a wide area from the South of the United States down to Paraguay and western Brazil. *Euchlaena* has the same chromosome number as *Zea*, i.e. 10, and both species are easily crossed with normal chromosome pairing and reasonable fertility in the hybrids. The basic chromosome number in *Tripsacum* is evidently 9, though all species known have either 18 or 36 chromosomes haploid, and aneuploid forms seem to exist in nature (Marajo Island, BRIEGER). MANGELSDORF and REEVES have shown that hybrids between *Tripsacum* and *Zea* may be obtained, though with considerable difficulty. There is no pairing in the highly sterile hybrids. The very close botanical relation between all three genera becomes specially clear when we study their ontogeny. Seed formation and germination are almost identical, though the correlations between main stalk and side shoots is different. The first stages in the development of inflorescences are identical, and in later ontogenetical stages *Euchlaena* and *Tripsacum*

resemble each other much more closely than either one does resemble maize (BRIEGER). In the triangle formed by these three genera, the relations between *Zea* and *Tripsacum* as two distinct forms seems rather clear, while the relative position of *Euchlaena* is rather more complex. In fact the genus has been considered, in former times, as an ancestor of maize, while recently MANGELSDORF has been inclined to consider teosinte as a descendant from maize. Some authors (COLLINS, BRIEGER) suppose that cultivated maize may have been a descendant of a cross between a *Tripsacum* species and another still unknown grass.

Nor does the distribution of primitive forms of maize help to clarify the question of the geographical location of the centre of origin. Since the time of Saint-Hilaire, pod corn has been considered as a "primitive" type. However, this statement needs revision. There is little doubt that the Tunicate factor, a dominant gene in the fourth chromosome of maize, should be considered as a wild type relic gene (MANGELSDORF, BRIEGER) which has been conserved by the Indians for special (ritual) purposes (CUTLER and CARDENAS). But the actual pod corn as it occurs sporadically in South America (Brazil, Bolivia, Colombia, etc.) represents a special form selected for special purposes, showing some characters of the T-factor in an exaggerated form (glume development especially) and others in a diminished form (abnormalities in tassel formation). Pod corn as such should thus not be considered as a primitive race, but as a specially selected domesticated form with a scattered general distribution (BRIEGER). Most pop corns may also be considered as still rather primitive, but their distribution again shows no relations to a centre of origin. There are pointed pop corns, with the base of the style transformed into a fine curved beak and conical ears with straight rows, in southern Brazil (Caingang and Guarani Indians) in Colombia (Boyacá) and in the Bolivian Andes. Pointed pop corn races with other forms of ear occur in Bolivia-Perú and in Mexico. The round seeded

pop corn races, generally with tightly packed kernels on cylindrical ears, appear also in widely separated regions, such as southern Brazil, Amazon Basin, Colombia, etc. MANGELSDORF concluded that part of the Bat Cave relics belonged also to a pop corn race. Thus it is quite evident that also the primitive pop corn races were distributed practically over the whole area of indigenous corn cultivation, without any concentration at any particular spot.

The same scattered distribution may be found for almost any other group of indigenous races of maize. Races with soft yellow kernels are characteristic of the following regions: a) Southern Brazil, Paraguay and eastern Bolivian lowlands represented by the race called "Guarani Soft Yellow"; b) Eastern Peru, North-eastern Bolivia and Central Brazil in the form of a race called "Soft Yellow Long Ear"; c) Colombia, spreading probably north into Central America and certainly south into Ecuador where we find other races under various names such as "Capiro Amarillo"; d) in the Southern United States finally in the race grown by the Pima-Papago. In all these cases the soft endosperm, though it should be yellow in accordance with its genetic constitution, has only a cream color, and the kernel color with its various shades of yellow to orange, brown or even red is caused by several genes, but mainly by alleles of the Bn locus, giving a pigmentation of the aleurone layer. Type of plant and type of ear differs in these races; the ear may be cylindrical or conical, row number may be low or high, though generally quite regular. The distribution of this group of races again does not give any indication of a possible centre of origin, but evidently we are dealing with a widely distributed type which suffered special selection in accordance with the preference of the local indigenous plant breeder in all characters except color and texture of the kernel.

The distribution of the dent races seemed for a long time to be much simpler with a limited area containing typical forms in Mex-

ico and Guatemala, spreading down into Colombia, though denting in various degrees occurs sporadically in many other regions. But two relatively new facts altered the situation. It was found that the Caingang of southern Brazil cultivate a very uniform white soft dent corn (BRIEGER). Furthermore it has been possible to obtain by selection from the non-dented "Guarani Soft Yellow" a typical dented soft yellow form. Thus we must suppose that the genes for denting are scattered over most or all of the whole maize area, and that the individual preference of the indigenous breeder has given origin to special dent varieties in widely separated regions.

The distribution of hard flint races follows the following pattern. There are three main areas, all in the Atlantic coastal region, where flint corn has been evidently the only or at least the preferred race: a) the "North-eastern Little Flints" of Canada, New England and New York; b) the "Orange-Yellow Flints" of the Caribbean area; c) the "Orange-Yellow Flints" in the South-East from Rio de Janeiro to the La Plata. The latter has been considered, without any proof whatsoever, as a post-Columbian introduction from Italy, but there is now only some doubt whether the Caribbean and South-eastern Flints should be regarded as one racial group or as two separated parallel indigenous developments. To these three races we should add some of other areas, where flint corn occurs besides other types, or even as a very secondary race: a) the "Big-grained Tropical Flint" which occurs from Guatemala to Colombia; b) two special varieties, Uchuquilla and Aizuma from the slopes in the Bolivian High Andes; c) a very hard white flint grown by the southern Guarani.

Thus in all these cases the distribution of racial groups points to a very general distribution of the genes responsible for all main types of maize, depending only upon the preference given by the indigenous breeder which variety or race predominates in any geographic region. We may, however, attempt in some cases to map out probable lines of pre-

historic dispersal and those point to the above-mentioned center of origin.

Thus the study of the actual geographical distribution of individual varieties or racial groups of maize does not give any indication of special concentrations in any limited area. We may ask next whether there are regions with a maximum concentration in the number of different races, or, in other words, whether there appear to exist centers of domestication of maize. VAVILOV developed his theory of collective centers of domestication, following DECANDOLLE, mainly for the domesticated species in the old world, and the distinction of American centers given in the newest map of DARLINGTON is rather vague. We must clearly distinguish, in our discussion, two types of centers: a) collective centers of origin or primary domestication, i.e. regions where a number of different species entered into cultivation, and b) individual centers of origin and domestication for any one species. There can be little doubt about the reality of the existence of the latter, though their localisation is in general quite difficult. Whether the collective centers, which represent the main issue of VAVILOV's theory, really exist, is a question to be discussed, and we shall try to separate such centers in the South American continent in order to be able to draw some general conclusions.

The region in the Central Andes occupied by the Inca Empire at the time of the Spanish conquest, is frequently considered as the most important center of origin, and PARODI mentions 43 cultivated species from this region. However, this list shows very clearly that the delimitation of the area is highly arbitrary. It comprises, following PARODI, at least three main climatical zones—a) the páramos above 3000 m, where a number of probably autochthonous species predominate such as *Chenopodium Quinoa* and *gallidicaule*, *Oxalis tuberosa*, *Ullucus tuberosus* and also potatoes, b) a lower region containing plants requiring a mean annual temperature of between 15° and 20° C, and c) a still lower region with a yearly average above 20° C, containing tropical species of

very wide distribution such as *Manihot utilisima*, *Ananas sativus*, *Psidium Guayava*, *Carica Papaya*, etc. In the intermediate region we find other widely distributed species such as beans, squashes, sweet potato, pepper, etc. The range of distribution of the members of the last two zones is such, throughout the tropical and subtropical part of South America, that there is no justification for drawing any line at the border of the Inca Empire, a line which would have been different if the Spanish conquistadores should have arrived either a few hundred years earlier or later. The high number of cultivated species in this relatively small area is mainly due to two factors, one anthropological or historical, i.e. the accumulation of a relatively dense, sessile and organized population, and the other biological, resulting from the extreme variation of ecological and climatic conditions, requiring specially adapted species in the páramos, on the slopes and high plateaus, and in the tropical valleys. A list from the Columbian area would probably show not much less diversity of cultivated species under a similar wide range of ecological conditions. In the eastern South American lowlands which include the Amazon Basin and a large part of the Paraguay-Paraná Basin, the number of cultivated species will be smaller since all species of higher altitudes do not find favorable ecological conditions. But the list of species grown even by so-called primitive tribes in Central Brazil is still quite impressive: *Manihot utilisima* and *Ipomoea Batatas* in several varieties as well as other root crops such as *Dioscorea*, "Cara", *Pachyrhizus*, several species of *Marantaceae* and *Araceae*, maize, peanuts (*Arachis hypogaea*), beans (*Phaseolus lunatus* and perhaps also *vulgaris*), squashes, cotton, pineapple, *Passiflora*, etc. With regard to all these tropical or subtropical species, there is no reason to suppose that their domestication occurred only in one special spot or region, and it seems to me much more likely that these species may have entered into domestication separately and in different places. Their later distribution and ex-

change still in very remote times was probably accompanied by subsequent local selection of special varieties or races or by what may be called "secondary domestication."

We come thus to the conclusion that nearly the whole area of the South American continent, between ten degrees north of the Equator to about 30 degrees south, should be considered as one South American collective center of domestication. The only area where agriculture had probably been developed outside this area, seems to be the zone of the Araucanian agriculture on the Chilean coast between about 35 and 43 degrees southern latitude; there a few, not widely distributed species were used, at least in a partially domesticated form, such as *Bromus Mango* and *Madia sativa* (PARODI). But this general conclusion leads us to the next question: whether the delimitation of such a large collective center has any biological meaning, a question which can be answered only after VAVILOV's asiatic collective centers have been restudied in detail. Returning to our main question, the origin of maize, we see that the delimitation of a huge South American collective center of primary domestication does not help at all to solve the problem, and this applies to any other cultivated plant of the continent.

However, we can say with certainty that this area does not contain a uniformly distributed mixture of maize races, but that geographically well defined areas of secondary domestication exist. On the whole it seems that these areas include mainly territory with comparable climatic conditions while ethnographic factors enter as a secondary agent.

The Pilcomayo-Paraguay-Paraná Basin in the South is divided into two regions: The area of the Southern Guarani (three races and many variants) and of the Caingang (3 races and variants). Further north, we find a large uniform area on the southern margin of the Amazon Basin at elevations between about 100 and 500 meters with one race and its variants grown by many unrelated tribes. Our collections from the Amazon Basin are

still incomplete, but there is at least one centre of domestication, near the mouth of the river, which evidently contained many races, which today are badly mixed. The coastal areas on the Atlantic seem to be divided into two regions, as mentioned already: that of the Caribbean Orange Flint and of the South-Eastern Orange Flint. The races of the Orinoco valley are so far unknown. In the Andean region, in the East, and, leaving out the Araucanians in the South, we have first the center of the Central Andes of Bolivia and Peru, containing a large number of races and variants divided into three climatic or ecological groups—the altiplano races, the flint races of the slopes, and the races of the higher valleys. Northern Peru and Ecuador include another region, not yet completely studied, of tropical races. The Colombian area is again divided into several climatic areas with numerous races, showing already very clear relations to the Central American areas (BRIEGER).

The theory of the individual centers of domestication includes the assumption that domesticated species should have in the center area the greatest degree of variability, as measured by the number of varieties or by the number of genes present. There seems to me little justification "a priori" for such an assumption. We know from modern studies on population genetics that the degree of genic variability, caused by the accumulation of mutations occurring at a constant low rate, depends upon a number of factors such as a) number of generations, b) number of individuals per generation, c) nature of the selective processes, leaving aside the importance of the mode of reproduction. Evidently in the center of origin and of primary domestication, the number of generations is certainly at a maximum, but the number of individuals per generation may be low and a rigidly defined trend in natural or artificial selection may result in the maintenance of only one or a few races in the zone of origin. On the other hand in secondary centers, where more individuals may

be grown and where both natural and artificial selection may follow diversified trends, a number of races may coexist, with a corresponding increase in genic variability. In fact the more densely populated zone of the Central Andes, where maize is grown from sea level under tropical conditions up to the altiplanos at about 3,000 meters, contains in a smaller area more races of maize than the much larger marginal area south of the Amazon, where only one principal race exists. But this does not justify the conclusion that the former could be considered as a primary and the other as only a secondary center of origin.

Furthermore, we find in the literature also the assumption that variability and number of varieties should diminish along the lines of dispersal and in proportion to the distance from the original center of dispersal. This hypothesis again finds no support in the distribution of the indigenous maize races. We mentioned already the scattered distribution of basic types such as pop corn, soft yellow maize, dented or flint maize, which can be explained only by a very uniform dispersal of the necessary genes and by the diversified nature of local selective trends.

In conclusion, it seems to me we can say that many of the aspects of the hypothesis on centers of origin, of domestication and of maximum genic variability are much too schematic and simplified to find support when applied to any special case, such as that of maize.

L. F. RANDOLPH (Ithaca, N. Y.)

*Crossability of Maize and *Tripsacum* in Relation to Theories of the Origin of Maize*

Following the successful hybridization of maize and *Tripsacum dactyloides*, a species native of the southern United States, MANGELS-DORF and REEVES developed a tripartite theory to account for the origin of maize based on the assumption that (1) the progenitor of cultivated maize was an unknown form of South American pod corn, (2) there was a later spread northward into Central America where

in recent times primitive maize hybridized with *Tripsacum* to produce teosinte, and (3) maize grown in the United States at the present time contains significant amounts of *Tripsacum* germ plasm. There is very little experimental evidence to support these hypotheses.

From extensive tests of the crossability of the various species of *Tripsacum* native to Central America and Mexico with the more primitive unimproved type of maize in the same regions it has been established that the maize and *Tripsacum* of these regions are highly cross incompatible. By utilizing a special embryo culture technique it was possible to obtain from repeated attempts, involving the testing of more than 120,000 gametic combinations, conducted from 1945 to 1949 only two hybrid seedlings from cross pollinating Mexican and Guatemalan forms of *Tripsacum* and maize. With the same technique hybrids were obtained readily from *Tripsacum dactyloides* and various types of corn grown in the eastern United States.

These results indicate that in Central America and Mexico, which is the center of diversity of the genus *Tripsacum* as well as a region in which there are numerous types of unimproved maize and teosinte, there has developed a very high degree of genetic cross incompatibility between maize and *Tripsacum*. It is concluded that primitive maize and *Tripsacum* probably have existed together without any appreciable amount of natural crossing for long periods of time in Mexico and the neighboring regions of Central America, and that maize probably originated in this area, which is the center of diversity of related genera.

Discussion

A. MÜNTZING: What significance should be attached to the data presented on cross incompatibility of *Zea* and *Tripsacum* in relation to the period of time during which failure of crossing of these two genera has prevailed in Mexico and Central America?

L. F. RANDOLPH: The tests of crossability

included several different species of diploid and tetraploid *Tripsacum* from widely separated areas and diverse habitats, isolated by very pronounced geographic barriers. The length of time required for genetic isolating mechanisms to have appeared by mutation and become widely distributed in the populations of these morphologically and cytologically different forms of *Tripsacum* can only be conjectured, but it can be conservatively estimated that at least several thousands of years must have been involved.

WERNER ROTHMALER (Halle/Saale) Die Taxonomie der Kulturpflanzen

Die Sippenbildungsvorgänge bei Wild- und Kulturpflanzen sind zunächst die gleichen, so dass sich Taxonomie und Nomenklatur der Kulturpflanzen denen der Wildpflanzen im allgemeinen unterzuordnen haben. Doch muss den Differenzen, die vor allem durch andere Selektionsprozesse hervorgerufen werden, bei den Kulturpflanzen Rechnung getragen werden. Sippen (taxons) entstehen meist durch Divergenz, wobei durch die Selektion grosse Lücken zwischen ihnen geschaffen werden, die eine leichte Trennung der Sippen von einander ermöglicht. Bei den Kulturpflanzen aber bleibt die Formenfülle zwischen den extremen Sippen meist als lückenlose Übergangsreihe erhalten. Dazu kommt, dass sehr häufig Kombinationen zwischen diesen Sippen eintreten, wobei die Lage noch dadurch kompliziert werden kann, dass weitere Arten mit ihrer Formenfülle ebenfalls in den Vermischungskreis eintreten, so dass sich keinerlei phylogenetisches oder lineares Bild mehr ergeben kann. Das sinnverwirrende, netzförmig verknüpfte Muster von Formen lässt keine natürliche, sondern nur noch eine künstliche Ordnung zu.

Es ist sicher abwegig in der Kulturpflanzen-taxonomie und Nomenklatur die Wege VAVILOVS (geographische Gliederung), SINKAJAS (oekologische Gliederung) oder PANGALOS (von Wildpflanzen unabhängige Gliederung) einzuschlagen. Wir müssen die Kulturpflanzen,

soweit es möglich ist, in das System der Wildpflanzen einordnen und dürfen nur dann davon abweichen, wenn es nicht anders möglich ist. So sollten wir den Begriff der Kulturpflanzen-sammelart (Cultplex nach JUZEPCZUK) verwenden (also *Musa sapientum* coll. statt *M. acuminata*-Kultursorten, *M. balvisiana*-Kultursorten und *M. sapientum* resp. *M. paradisiaca* oder *Ribes rubrum* coll. statt *R. houghtonianum*, *R. spicatum* etc., *Hordeum vulgare* coll. *Brassica oleracea* coll. etc.) Wenn natürliche, klare Unterarten (Subspecies oekologischer, geographischer, klimatischer oder sonstiger Isolierung) nicht unterschieden werden können, dann ist die Varietätengruppe (convarietas) als künstliche Zusammenfassung der Varietäten zu verwenden, denen sich dann Subvarietäten und Formen unterordnen können. Die niedrigste Einheit ist die Sorte (Linie, Strain, cultigen) wie sie schon immer klar unterschieden wurde.

ELISABETH SCHIEMANN (Berlin-Wilmersdorf)

Artbildung in der Gattung *Fragaria*¹

Nach einem Überblick über die heute bekannten Arten der Gattung *Fragaria* mit der Polyploidreihe $n=7$, wozu eine Anzahl neuer Chromosomzahlen gegeben wird, wird die genauere geographische Verbreitung, welche von meinem Schüler STAUDT ausgearbeitet ist, in Beziehung zur Morphologie und Cytologie, und dieser zur Geschlechtsverteilung besprochen. — Die ersten für Verwandtschaft und Artbildung wichtigen Kreuzungsanalysen von LILLENFELD und SCHIEMANN (1934 u. 1937) haben *Fragaria moschata* als einen Autohexaploiden erkennen lassen, 7+21 Chromosomen geben im Bastard durch kombinierte Allo- und Autosynthese 14 Bivalente und volle Fertilität. Während LILLENFELD das *F. vesca*-Genom (aus *F. nipponica*) zugrunde legt, baut SCHIEMANN die Analyse auf die Kreuzung *F. moschata* × *viridis* auf. Die nur sehr schwer gelingenden Kreuzungen *F. vesca* × *moschata* (reziprok nicht gelingend) haben nur 5 pentaploide Bastarde gegeben, 3 ♀♀

¹ Ausführlich publ. in Z. f. Pflanzenzüchtung, 30, 1951.

und 2 ♂♂. Doch ist auch 1 tetraploides ♂ mit funktionsfähigem Pollen entstanden, was der Lilienfeldschen Deutung entgegenkommt.

Dem unterschiedlichen Verhalten von *F. vesca* und *F. viridis* in *moschata*-Kreuzungen entspricht die bis zu 50 % gehende Sterilität des leicht und häufig spontan entstehenden F_1 -Bastards *F. vesca* × *viridis*, dessen Analyse bis in F_2 und F_3 leider in den vergangenen Jahren wiederholt unterbrochen und zerstört worden ist; sie kann erst jetzt mit den neuen Arbeitsmöglichkeiten wieder aufgenommen werden.

Die pentaploiden Bastarde haben gelegentlich aus funktionsfähigen Gameten spontan Ansatz gegeben, während künstliche Bestäubungen ohne Erfolg blieben. Im ganzen sind 5 Nachkommenschaften aus Pflanze 1535 erzielt. Eine erste Analyse der habituell sehr variablen, in der Blütenregion sehr einheitlichen, durch Blütenfüllung und fast völlige Sterilität ausgezeichneten Nachkommenschaft der Pflanze 1535 habe ich 1943 gegeben (Flora, 37). Es wird jetzt über eine 2. Familie aus Spontanansatz berichtet, in der, entsprechend KIHARAS Vermehrungs- und Verminderungsreihe bei Weizen, 3 verschiedene ± fertile Pflanzentypen und 3 verschiedene Chromosomenzahlen erscheinen: 1) *moschata*-ähnliche mit 42 Chromosomen, 2) mutterähnliche mit ± 35 Chromosomen und 3) der tetraploiden *F. orientalis*-ähnliche mit ± 28 Chromosomen. Starke Gruppenbindungen erschweren die genauen Zählungen. Die Untersuchungen der Meiosis hat noch zurückgestellt werden müssen: ein Teil der Stammpflanzen ist aber erhalten.

Dieses Resultat regte zur Analyse der tetraploiden *Fragaria orientalis* an, in die alles was an tetraploidem Material vorhanden ist, hereinbezogen ist, und welche mein Schüler G. STAUDT durchführt. Sie hat bereits eine Reihe wichtiger Resultate gebracht, welche auf die Beziehung zwischen *F. vesca-viridis* und *F. moschata* einiges Licht werfen. (Inzwischen publ. in Z. ind. Vererb.lehre, 84. 1952.)

Endlich wird über ein weiteres Auftreten tetraploider Pflanzen vom Gigastyp in einer *F. vesca* × *viridis* F_1 berichtet, welche dem Gigas-

typ der aus Colchizinierung gewonnenen tetraploiden *F. vesca* entsprechen, und im Habitus in F_2 und F_3 konstant geblieben sind.

Diese verschiedenen Typen des spontanen Auftretens von polyploiden Pflanzen in sterilen Kreuzungen stützen unsere Annahme über Entstehung der natürlichen Polyploidien und werden bei weitergehender Analyse entscheidendes über die Artbildung in der Gattung *Fragaria* aussagen können.

Die Vortragende bittet die Kollegen aus aller Welt um Vervollständigung des Sortimentes, ohne das eine endgültige Bearbeitung der Gattung nicht möglich ist, um Zusendung von Pflanzen oder besser von Beeren (einzeln auf Fliesspapier zerquetscht) von echt wilden Standorten mit genauer Angabe der Herkunft.

WERNER ROTHMALER (Halle/Saale)

Die „Gen“-Zentren der Kulturpflanzen

Die Zentren grösster Mannigfaltigkeit und der Häufung von Primitivformen der Kulturpflanzen, die z.T. schon seit dem Altertum die Menschheit beschäftigten, wurden von VAVILOV in seiner „Genzentren-Theorie“ erklärt. Diese und spätere Erklärungen, die vor allem im Zusammenhang mit der Chromosomentheorie der Vererbung vorgenommen wurden, treffen nicht zu. Diese deutlich unterscheidbaren Zentren sind rein menschlich, kulturgeschichtlich bedingt. Die Zentren decken sich mit den Gebieten, in denen der Ursprung menschlicher Zivilisation überhaupt zu suchen ist, wie Urgeschichtsforscher und Ethnologen überzeugend nachgewiesen haben. So gelten sie auch nur für alte Kulturpflanzen, die schon in vorgeschichtlicher Zeit in Kultur waren, während alle in späterer Zeit aufgenommenen Kulturpflanzen andere Zentren aufweisen (so z.B. die Futterpflanzen des 18. und 19. Jahrh. in Mitteleuropa oder die modernen Zierpflanzen). Sie gelten auch nur für Pflanzen, die zu den alten Anbaumethoden passen. So hat man z.B. in Peru nur ein Zentrum für Hackfrüchte, da man dort nur den

Grabstockbau kannte. Diese Zentren lagen wie die Ursprünge menschlicher Zivilisation in den Gebirgen und nicht in den fruchtbaren Ebenen; in den Gebirgen aber hielt sich der primitive Pflanzenbau mit der Fülle primitiver Formen, während in den Ebenen die Entwicklung der Menschen, seiner Anbaumethoden und seiner

Kulturpflanzen weiterschritt. So haben sich auch in sekundären Gebieten primitive Formen nur in Gebirgen gehalten, z.B. Springe in Portugal und in den Alpen oder primitive Getreide in Asturien, in den Alpen und in asiatischen oder afrikanischen Gebirgen.

SESSION 8

July 19th, 9 a. m. — noon, Attendance: 60 members

Chairman: G. E. BLACKMAN, Recorder: E. ÅKERBERG

SUBJECT:

Biology and Control of Weeds

EWERT ÅBERG (Uppsala)

Biology of Weeds and Hormone Weed Killers

Weed control with chemicals and by help of mechanical means cannot be successful unless germination characteristics of the weed seeds and the growth development of the weed seedlings are known. Investigations on germination biology like the recent ones by KOLK (1947) and VON HOFSTEN (1947) are therefore necessary and should be carried out more extensively. By knowing the germination biology of the main weeds it is possible to apply a correct soil treatment with mechanical means in order to bring out at the right time those seedlings which can be effectively killed by chemicals or by help of mechanical devices. Very likely the germination biology varies with the biotypes and there is an indication of this in VON HOFSTEN's investigations (1945) with differently colored mustard seeds. This must be investigated further. It is also necessary that now, since modern chemicals of the growth substance group are used in weed control work, the growth biology of the plants after the germination and seedling stage be studied. This is true for weeds as well as cultivated plants in which spraying is to be done.

Also in this latter type of investigation the biotype reaction must be followed.

It is well known that 2,4-D substances (2,4-dichlorophenoxyacetic acid) in general have a better effect than the methoxone substances (4-chloro-2-methyl-phenoxyacetic acid), but exceptions from this general rule may serve as illustrations of the necessity of studying the reaction of different species of weeds as well as cultivated plants to different substances and to do this with special emphasis on the reason for this different reaction. In a recent publication (HAGSAND and ÅBERG 1950) the reaction of *Galeopsis* spp. to different types of hormone weed killers was discussed on the basis of experiments in 1949. It could be shown that methoxone is much more effective against *Galeopsis* spp. than such 2,4-D substances as the 2,4-D ethyl ester and the 2,4-D triethanolamine salt. It could also be shown that the effect on the seedlings varies with the growth stage. Spraying at an early growth stage, i.e. the cotyledon stage with two true leaves, did not prove to be as effective as spraying at a later stage, i.e. when the number of true leaves had increased to eight. The difference in reaction might be caused by the amount of active substance that is absorbed by the plants with two leaves and by those

with a greater number of leaves. But it could also be that the composition of the cell sap in the plants varies from one growth stage to another and that the effect of the hormone weed killers depends on the cell sap composition. Artificial hormones, being used as weed killers, are in many respects related to the growth substances in the plants. Small variations in the amount and composition of the growth substances in the seedlings might be enough to cause variations in the effect of the artificially applied hormones (HAGSAND and ÅBERG 1950). This brings out the necessity of studying 1) the reaction of a number of species within different families against spraying with different artificial hormones, and 2) the reactions of the same species to the same hormone at different stages of growth. The latter type of studies has been going on for a couple of years and it is quite well known in what stages for example small grains and flax should be treated (PEDERSEN, ANDERSEN og HERMANSEN 1948; ÅBERG 1949; ANDERSEN and HERMANSEN 1950).

It would be of great value if the production of growth regulating substances within the plants could be determined. This has proved to be very difficult with the methods now available for such determinations. It is, however, also necessary to learn more about the components of the different hormone weed killers. Often abnormalities in cultivated plants or different effects on weeds have been referred to the inert substances of a hormone weed killer. This might or might not be correct. SJÖBERG (1950) has shown the great variation in composition of chemicals of the methoxone type which were used in weed control work in Sweden. If the differences in composition can be as marked as shown in table 6 in SJÖBERG's paper it is also necessary to try to find out how different components behave against weeds as well as cultivated plants.

Preliminary studies were carried out at the Institute of Plant Husbandry, Royal Agricultural College of Sweden, during 1949 and 1950. They were started as laboratory work. Seeds

of different plants were tied into a small bag of thin cloth and hung from the stopper in an Erlenmeyer flask so that it hung in the middle of the flask. The chemical substances were put at the bottom of the flask and the stopper was so fixed that the volatile parts of the chemicals would remain in the flask. Both methoxone and 2,4-D were used but so far only components of methoxone have been studied. Red clover, swedes, barley and penny cress were studied in this type of experiments. The results from the experiments clearly show that there is a different effectiveness of the components. Thus 4-chloro-2-methyl-phenol is more effective than 6-chloro-2-methyl-phenol, and 4-chloro-2-methyl-phenoxyacetic acid more effective than 6-chloro-2-methyl-phenoxyacetic acid. The 2-methyl-phenoxyacetic acid is far from as effective as the chlorinated phenoxyacetic acids. Orthocresol seems to have about the same effect as 4-chloro-2-methyl-phenol. The 6-chloro-2-methyl-phenoxyacetic acid seems to promote growth of fungi more than the rest of the components.

Observations in field plots and in pot experiments during the summer of 1950 showed close agreement with the results from the laboratory and, in addition, especially emphasized that the 4-chloro-2-methyl substances are harder in their effects than the 6-chloro-2-methyl substances. It is necessary to enlarge the investigations on the influence of the components of the hormone weed killers in order to get closer to the answer explaining why plant species behave differently and why plants in different growth stages react with different symptoms.

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SIGURD ANDERSEN (Köbenhavn)
*Using Hormone Derivatives at Different
Stages of Development of the Cereals*

A decrease in the yield of grain can be brought about at any stage of development by using sufficiently large quantities of hormone.

Abnormalities in straw and ear occur only when the cereals have reached a certain stage of development at the time of spraying. At this time very small quantities may produce a great effect, while at other times even very large quantities have no effect.

Abnormalities in the straw occur after spraying immediately after the emergence and are most frequent at this time. Abnormalities in the ear occur after spraying at a later stage of development. The ear is highly susceptible to hormones at a certain stage of development and the susceptible period lasts about 10 days. Before and after this period none or very few abnormalities appear. Barley is highly susceptible when the plants have about three leaves, while oats seems to be susceptible at a somewhat later stage of development.

The time of spraying, e.g. the development of the ear, influences the type of abnormality, and by early spraying in barley and wheat the abnormalities appear in the lower part of the spike, while they appear farther up in the spike in plots sprayed at a later date.

From the figures the conclusion may be drawn that spraying with hormones has a serious effect on primary meristem which are just beginning to form a new organ.

Counting the leaves of young plants of barley and oats has proved to be a good method in determining the stage of development of the ear. The method consists in counting the leaves of 50 plants, and the standard error has been found to be ± 0.059 leaves.

Discussion

H. OSVALD: Dr. ÅBERG touched a rather important problem in his paper, that is the composition of modern weed killers. I can freely admit that at the Institute of Plant Husbandry we did not realize, when we started experiments with these substances, that the composition varies as much as has been subsequently shown. We did not have the opportunity to use the pure chemical substances, but had to rely upon the commercial preparations. Many differences in the results obtained in different years may be explained by the variation in the composition of the commercial substances. I can mention another series of analyses. 14 samples of a commercial weed killer, which should contain 7.5 per cent of methoxone, were analyzed and it was found that the content of the active substance varied from 4.0 to 7.5 percent. In this situation I think that scientists engaged in this research should require a registration and declaration scheme. Otherwise we will never be able to rely upon the substances on the market.

H. W. HOWARD asked whether any carry-over effect to the next generation had been found when seeds from the abnormal plants were grown in the following year, since SPRAGUE in America had found such an effect in maize.

M. JOHNSTON: What were the actual formulations of 2,4-D compounds used in the experiments described and were not differences found in the action of the 2,4-D formulations themselves?

F. T. WAHLEN: Can the two speakers give any indication as to the extent to which hormone weed killers are used in the farming practice of Scandinavian countries? And regarding the types most prevalent in use?

EVERT ÅBERG: Ever since we started our work on abnormalities in cultivated plants as caused by hormone derivatives we have also followed the after-effect on seedlings from kernels in abnormal heads. We have never been able to show as yet that there have ap-

peared any abnormalities that carry over from one generation to the next.

Why the Swedish varieties are not as resistant as the English ones may perhaps have something to do with the conditions under which they are grown. Different climates and perhaps, above all, the speed of growth influences the results. We must not forget these factors and we should compare the varieties under equal environmental conditions.

SIGURD ANDERSEN: I agree with Dr. ÅBERG. We have sown kernels from abnormal spikes, and we found no abnormalities in the next generation.

A difference between varieties is difficult to measure, because you need to spray the different varieties at exactly the same stage of development.

We used Herbattox and Agroxone in our experiments. Herbattox is manufactured in Denmark and contains the sodium salt of 2,4-D. In 1950 approximately 15 % of the area grown with grain in Denmark was treated with hormones. Most of this area was treated with preparations containing the sodium salt of UCPA.

A. E. TRAAEN (Vollebekk)

Injury to Norway Spruce Caused by Calcium Chloride Used against Dust on Roads

In the spring of 1939, report was received about considerable damage on spruce trees along a main highway in Ostfold in Norway. An inspection showed that many of the spruces nearest to the road had reddish-brown needles on the side facing the road, whereas the needles on the opposite side were, for the most part, healthy and green. Because of the one-sided effect, it seemed reasonable to assume that the injury was not produced through the roots. The road had been treated with "Dammol" and later with calcium chloride. In one particular spot where the road made a slight curve, even the tallest trees were discolored right to the top. On the day of inspection the roadbed was very dry, the au-

tomobiles leaving large clouds of dust behind. When the cars turned off in the mentioned curve, the dust clouds continued straight ahead, the tall trees growing there being powdered with dust to the very top.

A microscopic examination of the brown needles showed morbid changes in the interior cells of the needles.

A series of experiments was conducted to ascertain the effect of calcium chloride on spruce. This was done, partly by spreading the pulverized substance upon the needles, partly by sprinkling it on the ground above the roots.

The results of the first-mentioned experiments varied greatly, depending not only upon the quantity of calcium chloride used, but even more upon the precipitation. The length of the interval between application and first rainfall was especially important, also the amount of rain received.

When the material was dusted onto the needles, it very rapidly absorbed humidity from the air, even in dry weather, thus making the needles moist and shiny.

Already after 5-6 days the effect became clearly apparent. Very often discoloration did not take place of the powdered needles themselves, but of the branches below, or of the needles upon the inner section of the powdered branches. In these cases rain had washed the calcium chloride off the most exposed parts. Even less than 1 mm of precipitation during the first few days after an application was enough to prevent injury.

Experiments with feeding calcium chloride through the roots gave the following results: No visible injury was caused to large trees by applications up to 8 kg. Smaller trees displayed the previously mentioned symptoms, the degree of injury depending upon the size of the trees and the quantities applied. Trees 1 m tall were somewhat damaged by 1/4 kg, and trees 2 m tall by 1/2 kg.

A chemical analysis proved that the injured needles contained far more chlorine than the healthy ones, this being true both of the ex-

perimental trees and the spruces along the road in Ostfold.

Discussion

OLOF SVANBERG: In another case of anti-dust spraying on roads, curiously enough, this measure may be in favour to the vegetation. This occurs in Sweden when bisulphite waste from the paper factories is spread on roads surrounded by light sandy soils with manganese deficiencies in the crops. In such cases one may see a healthier vegetation in the fields near the roads.

E. K. WOODFORD (Oxford)

The Assessment of Relative Toxicity and the Evaluation of Selective Herbicides

The discovery that growth regulating compounds could be used for the destruction of undesirable species in a plant community revolutionized thought and practice in chemical weed control and stimulated research into the evaluation of new and old herbicides. But despite the fact that statistical methods have been devised and accepted as standard practice in the assessment of fungicides, bactericides and insecticides, little attempt has been made to use them in the evaluation of herbicides. In consequence much of the work in this field has been of an empirical nature and it is often impossible to judge the accuracy of the results obtained.

Before it is possible to assess with precision the efficiency of selective herbicides it is essential to consider their possible mode of action and to appreciate the factors responsible for the selective toxicity. Although there is a lack of precise information on the ways in which herbicides cause the death of plants, it is usually sufficient for the purposes of evaluation to know whether they act as growth regulating substances, and whether they are translocated in the tissues that they affect. The factors responsible for selective toxicity have been discussed by BLACKMAN (1) and depend

upon differences in (i) retention and persistence of the herbicide on the aerial parts of the plant or in the soil, (ii) penetration into the shoot and uptake by the root, (iii) translocation within the plant, and (iv) toxicity at the site of action. Most modern herbicides are dependent upon a combination of these factors for their selective action. The detailed evaluation of their efficiency will in consequence depend upon a study of each of these aspects.

A single laboratory or greenhouse screening test is therefore completely inadequate. Such tests based on the inhibition of germination, reduction in growth or kill of seedlings and tissues are bound to overlook many promising compounds.

Because there are so many factors influencing selective toxicity and because of the consequent difficulty of assessing them in the laboratory or greenhouse, most evaluations are carried out in the field by applying the herbicide in the manner which it is assumed will be used in practice. Such experiments, although they give immediate answers, are not completely satisfactory because they do not permit the study of the separate facets of selectivity and in consequence limit the generalizations that can be drawn from the results.

At Oxford we have been comparing the toxicity of different groups of compounds on a range of tissues and microorganisms as well as on whole plants and associations of plants, in an attempt to separate out the various components of overall selective action.

Although such experiments may be very varied in their method of execution, they can be separated into two distinct types with respect to experimental design and method of statistical analysis. First, Screening Experiments which are concerned with the general effects of different herbicides and the reactions of different plants or plant tissues. These usually rely on comparisons of the effect of a single dose applied to a plant or tissue at a definite stage of growth. Their usefulness in determining the relative efficiency of selective

herbicides is limited and can be misleading. Second, Dose-Response Experiments which involve the detailed evaluation of the dose-response relationship and necessitate the measurement of the effect of many more dose levels than is required in screening experiments. Statistical methods for dealing with the dose-response curves obtained by the probit transformation have been described by FINNEY (2) and make possible accurate comparisons of toxic action.

The nature of the dose-response curve and the usefulness of the probit transformation in the evaluation of plant toxicity data is discussed in the following section of this paper and is illustrated by examples from the work of the Agricultural Research Council Unit of Experimental Agronomy at Oxford.

If a single herbicide is applied at a number of different doses to batches of uniform experimental material, and the proportion of plants killed in each sample is calculated and plotted against dose, it is usually found that the points lie on a smooth sigmoid curve increasing steadily from no kill at a low dose to a 100% kill at a high dose. Such a curve would be expected if each individual plant required a critical dose-level to kill it. An example is shown in Fig. 1 (A) where the percentage kill of pea plants is plotted against the dose of 2,4-dinitro-6-secondary butyl phenol (DNBP) applied as an oil emulsion. In practice the dose levels of greatest interest are those at the extremities of such curves; doses that will kill all the weeds and yet have no effect on the crop. From the sigmoid nature of the dose-response curves it is obviously very difficult to assess the required quantities with any degree of precision. The dose which kills 50% of the plants (L.D. 50) is the measurement which can be determined with the greatest accuracy and it is this quantity which is generally employed for accurate comparisons of toxicity.

If the percentage kill is plotted against the logarithm of dose (dosage) a normal sigmoid curve is obtained (Fig. 1 (B)). Then, if the

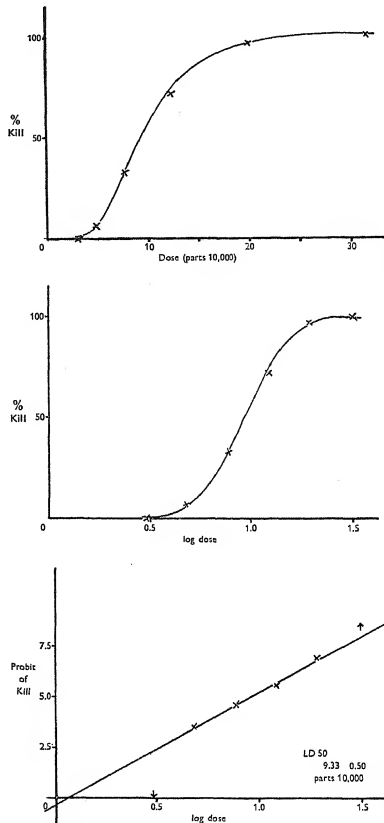


Fig. 1. The relationship between dose and percentage kill. Pea plants sprayed with 2,4-dinitro-6-secondary butyl phenol (DNBP). A. Sigmoid curve, B. Normal Sigmoid curve, C. Probit regression line.

data of percentage kill are transformed into probits a close approximation to a straight line is obtained (Fig. 1 (C)). The parameters of this line can be calculated and the L.D. 50 or any other level of response determined, together with their estimates of error.

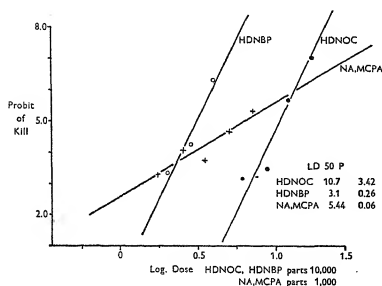


Fig. 2. Probit regression lines of the toxicity of 3,5-dinitro-o-cresol (DNOC), 2,4-dinitro-6-secondary butyl phenol (DNBP) and sodium 2-methyl-4-chlorophenoxyacetate (NaMCPA) to Linseed (*Linum usitatissimum*).

The slope of the probit regression line is a measure of the variance of the distribution of the critical values. Usually probit regression lines for herbicides which act in the same way are parallel and it is possible to estimate with precision the relative toxicity of such compounds over all levels of kill. The results of an experiment in which seedlings of linseed (*Linum usitatissimum*) were sprayed with a range of concentrations of two aryl nitro compounds 3,5-dinitro-o-cresol (DNOC) and 2,4-dinitro-6-secondary butyl phenol (DNBP) and a growth regulating substance, sodium 2-methyl-4-chloro-phenoxyacetate (NaMCPA) are shown as probit regression lines in Fig. 2. The lines for DNOC and DNBP are parallel, DNBP being 3.42 ± 0.26 times as toxic as DNOC. The slope of the probit line for NaMCPA is much less steep and this difference indicates that they do not all act in the same way. It is, therefore, only possible to compare the relative toxicities of the two types of herbicides at a particular response level and the level chosen will determine the figure obtained.

The slopes of probit lines are influenced by many factors, such as uniformity of the plant populations or method of treatment application. Such slopes are sometimes useful indications of variations in response which would

have been missed if L.D. 50 values only had been compared.

An example of the way in which probit regression lines can be used to detect the differential effect of environmental factors on two herbicides is given in Fig. 3. A uniform stand of *Raphanus raphanistrum* growing in spring wheat was sprayed on four occasions with a range of concentrations of DNOC and DNBP. The calculated probit regression lines for each compound on each occasion had a common slope and the relative potency (P) was substantially the same on the first, second and fourth spraying dates, but significantly higher on the third date.

Date	Plant Stage	Slope Probit Regression	Relative Potency
1. 19 April	2 leaves	2.61 ± 0.7	3.8 ± 1.4
2. 3 May	4-6 leaves	2.61 ± 0.6	3.0 ± 0.7
3. 14 May	8 leaves	2.61 ± 0.5	5.0 ± 1.4
4. 27 May	Early Bud	2.74 ± 0.5	3.8 ± 0.5

It is apparent from the position of the lines in Fig. 3 that on the third occasion the toxicity of the DNBP spray was relatively much higher than that of DNOC. The weather records show that on May 14th the maximum temperature was 10°F higher and the minimum 6°F higher than on any of the other spraying dates, and that in addition May 14th was in the middle of a spell of dry hot weather. There is therefore a strong indication that the toxicity of DNBP is more affected by environmental temperature effects than DNOC.

Where we have measured the quantal response of death, we have generally obtained dose-response data which give straight lines with the probit transformation. Many measurements of toxicity however are concerned with quantitative data which are often more difficult to deal with statistically because the dosage response curve is not always a normal sigmoid. Nevertheless, it is always possible to obtain a dosage-response curve and to compare the toxicity of equi-effective concentrations.

Results from experiments on the inhibition of germination, suppression of root and shoot

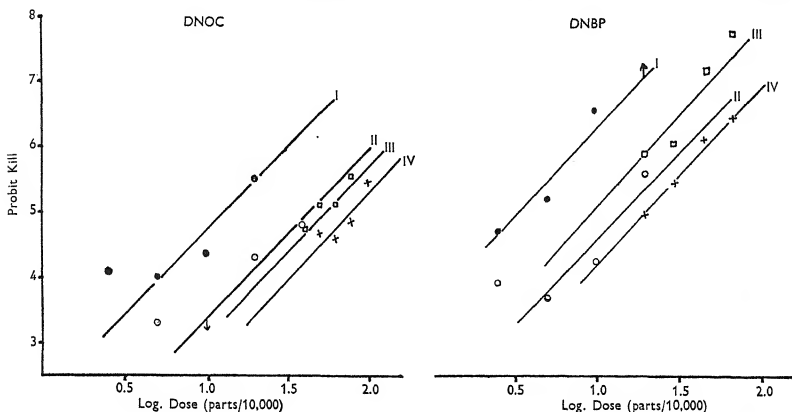


Fig. 3. Probit regression lines for 3,5-dinitro-*o*-cresol (DNOC) and 2,4-dinitro-6-secondary butyl phenol (DNBP) for kill of *Raphanus raphanistrum* on four spraying dates.

growth often give normal sigmoid dosage-response curves. In our research we have employed the water plant, *Lemna minor* extensively as a test organism. The increase in frond number can be taken as an index of growth and when the logarithm of frond

number is plotted against time a linear relationship is obtained. When nitro compounds are used as toxicants in the culture solution the slopes of the growth curves are a function of the concentration of the toxicant in the culture solution. Results obtained in this way

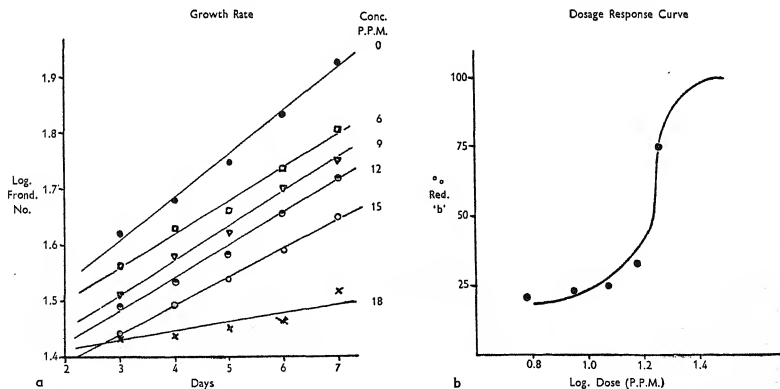


Fig. 4. Growth rates of *Lemna minor* grown in culture solution containing different concentrations of 2,4-dinitro-6-secondary butyl phenol (DNBP) and the dosage response curve obtained from the plot of percentage reduction in growth rate and logarithm of dose.

with DNBP are shown in Fig. 4 a. A dosage response curve can then be constructed by plotting the percentage reduction in the slopes (C) against the logarithm of the concentration of DNBP (Fig. 4 b). In this instance the curve is not a normal sigmoid, except at low dose levels, and it is therefore impossible to use the probit transformation. It is possible, however, to determine the dose required to reduce the growth rate by 50%, and to compare in this way the equi-effective concentrations of different compounds.

Summary

Many of the experiments on the assessment of relative phytotoxicity that have been reported in recent years have been based on the comparison of toxicity at one or two dose levels. Little attempt has been made to compare dose levels required for equi-toxic action or to use the statistical methods of probit analysis which have been devised for the assessment of insecticides and fungicides, but have been shown to be just as valuable for herbicides. In consequence, because of the lack of this statistical approach, it is often impossible to judge the accuracy of the results reported.

The nature of the dose-response curve in experiments based on the quantal response of death are presented in order to illustrate the usefulness of the probit transformation in defining the accuracy of the results obtained and in indicating the influence of environmental factors. Quantitative measurements of response often—but not always—give normal sigmoid dosage response curves. An example of a dosage response based on the reduction in the growth rate of *Lemna minor* caused by DNBP is presented as an example of the type of data obtained from quantitative measurements.

References

- BLACKMAN, G. E. The principles of selective toxicity and the action of selective herbicides. Science Prog. 1950.
FINNEY, D. J. Probit analysis. Cambridge Univ. Press 1947.

Discussion

HUGO OSVALD: Since I have not studied myself the herbicides by the method described by Dr. WOODFORD, I am not able to discuss the results obtained. But I should like on this occasion to congratulate the BLACKMAN team for the valuable contribution to the improvement of the research method, to the interpretation of the results and to the presentation of the experimental data. At my institute we shall in future employ the same method as much as possible.

OLOF SVANBERG: Are not the curves presented by the author necessarily dependent on a rather great number of different factors, such as the nutritional condition of the plants? A good nutritional condition must be in favour of their resistance, whereas a malnutrition will give rise to a greater sensibility. For this reason, the effects in the field may be able to bring surprises.

L. LING: L D 50 has been used satisfactorily in fungicidal tests which usually deal with large populations. In tests with high plants, how large should be the population in order to apply L D 50 significantly?

E. K. WOODFORD: The nutritional status of the test plant may have an effect on the plant's reaction to the herbicide but it cannot be assumed that a good nutritional condition will be in favour of resistance and vice versa.

It is not possible to state how large a population of plants is required in order to obtain significant L.D.50 figures. This depends on the uniformity of the plant material and many other factors. In our greenhouse tests with *Brassica alba* seedlings we like to use four pots, each containing about 25 seedlings, for each of the doses. At least five doses are used to obtain the dose-response curve.

ANNA MAURIZIO (Liebefeld-Bern)

Bienenvergiftungen mit pflanzlichen Wirkstoffen

Massensterben von Bienen können nicht nur durch ansteckende Seuchen, sondern auch

durch Erkrankungen nichtansteckenden Charakters verursacht werden. In der Regel handelt es sich dabei um Stoffwechselstörungen oder Vergiftungen, die meist aufs engste verbunden sind mit den von den Bienen gesammelten Nahrungsstoffen. In der Imker-Praxis sind seit langem zwei Gruppen solcher nichtansteckender Störungen bekannt, die nach ihrem zeitlichen Auftreten als „Maikrankheit“ und „Waldtrachtkrankheit“ (Schwarzsucht, Paralysis) bezeichnet werden. Es kann heute nicht mehr bezweifelt werden, dass diese Störungen zwar äusserlich ähnliche Symptome aufweisen, jedoch auf völlig verschiedenen Ursachen beruhen. Einige darunter sind auf Vergiftungen mit pflanzlichen Wirkstoffen zurückzuführen und werden als Trachtkrankheiten oder Trachtvergiftungen bezeichnet.

Die Honigbiene ernährt sich ausschliesslich von pflanzlichen Produkten. Als Kohlehydratquelle dienen ihr Nektar und Honigtau; der Bedarf an Eiweiss, Fett, Mineralstoffen und Vitaminen wird aus dem Pollen von Phanerogamen gedeckt. Alle drei Produkte kommen als Träger von giftigen Wirkstoffen in Frage.

Charakteristisch für Trachtvergiftungen ist, dass sie nur in gewissen Gegenden und Jahren vorkommen und dass ihre Dauer auf die Blütezeit, oder die Zeit der Honigtauabsonderung, der wirksamen Pflanze beschränkt bleibt. Voraussetzung für das Zustandekommen einer Trachtvergiftung ist, dass in einer Gegend grössere Bestände von Pflanzen wachsen, deren Produkte für Bienen schädlich sind.

Eine Massenvergiftung tritt jedoch auch hier nur ein, wenn die Bienen unter dem Einfluss äusserer Faktoren gezwungen sind, diese Pflanzen einseitig zu besuchen und sich in der Folge einseitig mit ihren giftigen Produkten zu ernähren. Die verbreitetsten und bisher am besten bekannten Trachtvergiftungen sind:

1) *Ranunculaceen-Vergiftung*. Beobachtet in der Schweiz, als Folge einseitiger Pollentracht von *Ranunculus puberulus* Koch und anderer Ranunculaceen. Wirksamer Stoff Anemonol.

2) *Aesculus-Vergiftung*. Beobachtet in Kalifornien bei einseitiger Tracht von *Aesculus californica* N. Giftig für Bienen sind Nektar, Honig, Pollen und Honigtau der Pflanze. In Europa kommen gelegentlich Bienenvergiftungen bei einseitiger Tracht von *Aesculus hippocastanum* L. und *A. Pavia* L. vor. Wirksame Stoffe wahrscheinlich Saponine.

3) *Tilia-Vergiftungen*. Beobachtet in verschiedenen Ländern Europas bei einseitiger Lindentracht, besonders von *Tilia tomentosa* Mönch. Schädlich sind Pollen, Nektar und Honigtau. Wirksamer Stoff unbekannt, eventuell Saponine.

4) Weitere, bisher nicht näher bearbeitete Trachtvergiftungen sind aus Nordamerika und Europa bekannt geworden bei einseitiger Tracht von: *Sapindus emarginatus*, *Veratrum californicum* und *album* L., *Astragalus lentiginosus*, *Hypericum*-Arten, *Fagopyrum sagittatum* Gilib., *Digitalis*-Arten usw.

5) Schädlich für Menschen, jedoch wenig wirksam für Bienen ist Honig von *Rhododendron ponticum* L. und *Kalmia latifolia* L. (wirksamer Stoff Andromedotoxin), *Euphorbia*-Arten, *Tripetaleia paniculata* und Honigtau-Honig von *Coriaria arborea* Lindsay (wirksame Stoffe Picrotoxin, Mellitoxin, Tutin).

Discussion

OLOF SVANBERG: Die Mitteilung Dr. MAURIZIOS ist deshalb besonders wichtig, weil man bei Bienenvergiftungen nunmehr im allgemeinen darauf völlig eingestellt ist, dass Behandlungen der Kulturvegetation mit den modernen Pflanzenschutzmitteln die Ursache gewesen sind. Dr. MAURIZIO hat unsere Aufmerksamkeit darauf gerichtet, dass die Anwendung der Pflanzenschutzmittel für die Bienen belanglos sein kann, vielleicht auch in solchen Fällen, wo die Bienenbesitzer diese Behandlungen in starken Verdacht ziehen möchten.

HUGO OSVALD: Zu dem letzten Teil dieses interessanten Vortrages möchte ich nur sagen—weil die Zeit jetzt beschränkt ist,—dass mit der rasch steigenden Verwendung von

Herbiciden, Insecticiden usw. die Frage des Bienenschutzes eine sehr wichtige ist. Ich möchte auch fragen, ob Dr. MAURIZIO Erfahrungen über die Wirkung des Honigs von *Acer platanoides* hat. Ich habe in meinem Garten viele verschiedene Bäume, u. a. *Acer platanoides* und Rosskastanie. In der Zeit wenn *Acer* blüht sterben die Bienen in grossen Mengen. Es ist in Schweden behauptet wor-

den, dass die Blüten von *Acer platanoides* einen giftigen Wirkstoff enthalten.

A. MAURIZIO: Die durch Trachtvergiftungen hervorgerufenen Bienenschäden sind sehr gering im Vergleich zu den durch moderne Schädlingsbekämpfungsmittel verursachten. Über Bienenvergiftungen während der Blütezeit von *Acer platanoides* ist mir nichts bekannt.

SESSION 9

July 19th, 1—4 p. m., Attendance: 50 members

Chairman: E. BOYKO, Recorder: E. ÅKERBERG

SUBJECT:

Minor Elements and Tracer Methods

R. SCOTT RUSSELL (Oxford)

Studies in the Absorption and Utilization of Phosphorus by Tracer Methods

Using radioactive phosphorus preliminary studies have been made of the absorption and utilization of phosphorus by young barley plants treated for short periods with very dilute culture solutions. Concentrations of labelled phosphorus varying from 30 to 0.0003 p. p. m. have been employed in experimental periods of from 1 hour to 7 days. In all experiments plants at the second leaf stage which had been raised in phosphate-free culture media were employed.

On account of the wide concentration range, plant uptake is conveniently considered as relative absorption, i.e. phosphate uptake expressed as a percentage of the initial content of the culture medium. When intact plants are treated with labelled phosphate for periods exceeding six hours a curvi-linear relationship has been found between relative absorption and concentration, with a well marked maximum at intermediate concentrations (usually in the order of 0.3 to 0.1 p. p. m.). The

decrease in relative absorption at the higher concentrations agrees with the results of many previous workers. The progressive reduction in relative absorption as concentration is reduced below 0.1 p. p. m. however shows that, contrary to expectations, the rate of absorption under such conditions is not proportional to concentration and that some other factor is limiting absorption. This result has been shown neither by detached root systems nor by intact plants in experimental periods of three hours or less.

The proportion of absorbed phosphate retained by roots and especially by meristematic tissues is inversely related to the concentration of the culture medium. When plants are transferred to phosphate free media, phosphate loss, relative to plant content, is greatest in plants previously treated with the lowest phosphate concentrations. Under such conditions, shoot-content increases in plants which have been treated with concentrations of phosphate of 0.1 p. p. m. or lower and decreases in plants treated with higher concentrations.

The pre-treatment of plants with unlabelled

phosphate increases the amount of labelled phosphate translocated to shoots from the more dilute media (0.0001 p. p. m.) in experimental periods of 24 hours. Root content is little affected.

These preliminary results indicate that the proportion of the phosphate entering the roots of plants which is retained therein against upward translocation is inversely related to the phosphate status of the plants. Phosphate thus retained is lost to the outer medium to a greater extent than other phosphate fractions. It is considered that the reduction in relative absorption observed when the external concentration is reduced below 0.1 p.p.m. P is due *not* to a reduction in the relative rate of primary absorption, but to the relatively greater outward movement of recently absorbed phosphate. More detailed discussion is inappropriate until the results are available of experiments undertaken to determine the relationship between phosphate retention in metabolism in roots.

Discussion

OLOF SVANBERG: One might raise the question whether not a number of problems studied with labelled phosphorus could be attacked just as well without the aid of this substance, in a classical chemical way. I cannot, however, say that Dr. RUSSELL has overlooked this fact, I think he has not.

Dr. RUSSELL's lecture gives rise to the question about the effect of different substances in the plant on the movement of phosphorus. I think especially of magnesium, known to be favourable for this movement. It would be of a great interest to find a quantitative assessment on this point.

R. SCOTT RUSSELL: I entirely agree that it would be interesting to study the effect of calcium and magnesium on phosphate distribution under our conditions. We intend to substitute both this and other cations for potassium in future work, but hitherto no such experiments have been carried out.

D. MULDER (Wilhelminadorp)

The Distribution and Causes of Nutritional Diseases of Fruit Trees in the Netherlands

In relation to fruit growing we have to consider four main types of soil:

1. river clay
2. marine loam
3. fluvio-glacial sand and marine sand
4. loess.

The oldest fruit growing areas are the river clay area along the big rivers Rijn, Waal en Maas and the loess area in Zuid Limburg. On the river clay we find potash deficiency due to potash shortness, potash fixation and magnesium excess in this soil. The loess does not give rise to a deficiency disease itself but sometimes the calcareous rock is underneath on a small depth and then we find iron deficiency.

Most of our nutritional troubles arise on the marine loam soils. The magnesium-potash relation is out of balance there by shortness of magnesium and excessive potash fertilizing. Moreover excess of calcium causes iron and manganese deficiency to be frequent and sometimes severe. On very light loams abundant fertilizing with superphosphate has resulted in a zinc deficiency which is locally very severe, specially in some orchards on Zuid-Beveland.

Characteristic symptoms of boron deficiency which could be expected on such a soil do not occur.

After having started cultivating fruit trees on loamy soils people tried the fluvio-glacial sands and the marine sands. The culture on fluvio-glacial sands was in many places a failure because of the copper deficiency. Also on marine sands there can occur copper deficiency but this is more rare. On all sands it is rather easy to get magnesium deficiency symptoms if potash is added.

The fact that so many nutritional disorders did arise in fruit culture may be attributed to the following circumstances:

1. After having taken into culture the best soils in the river clay and the loess, people settled down on less fertile areas like the marine loams and the sands.

2. The decrease in the use of organic manure and the increase of the use of artificial fertilizers causing a disequilibrium between the organic and the mineral content of the soil and between the different nutrients themselves.

3. The increase in density of the culture (stayer and filler system).

4. The use of sensitive varieties like Cox Orange Pippin.

The economic importance of these disorders is varying widely. Some are a threat to the life of the tree, like copper and zinc deficiency. The greater part is reducing both quality and quantity of the harvest. Some influence especially the keeping quality, like phosphate and nitrogen. Manganese deficiency is probably the most wide-spread but of minor importance. The rôle of boron in relation to bitter-pit is still uncertain. VAN STUIVENBERG (1950) could diminish the amount of bitter-pit by spraying at a certain date with borax.

The control of nutritional diseases has to be done in two ways.

1. the short direct way of spraying or injecting trees with the lacking elements.

2. the long way of fertilizing and altering soil conditions.

Control of the deficiency by spraying is possible for magnesium, manganese and zinc. Injection is still the only way in case of iron deficiency.

Discussion

D. J. D. NICHOLAS: With regard to the correction of Mn deficiency in fruit trees in England, foliage sprays of dilute manganese sulphate solutions have been very effective but soil applications of the salt have been relatively ineffective. Dr. MULDER appears to

find that soil applications of manganese sulphate corrected Mn deficiency. I would like to ask him whether the soil contained free calcium carbonate and abundant organic matter as under those conditions most of the manganese sulphate is immobilised?

Contrary to results obtained in England, Dr. MULDER finds that bitter-pit in apples is caused by boron deficiency. I would like to ask whether he determined the B content of the fruit from normal or bitter-pit trees or whether he had water only controls to confirm that the foliage swamp with boron was specific.

OLOF SVANBERG: Mr. MULDER's lecture attracts attention to a great number of important questions. We have to congratulate Dr. MULDER not only on his interesting lecture but also on the very important inventory work carried out in the Netherlands.

According to deficiencies in manganese in fruit trees "perhaps caused by the organic substances in the soil" it is a matter of interest, if this kind of deficiency is observed only in very young trees or in older ones as well?

In the cases of magnesium deficiency on sandy soils, have you made use of the French dolomite-(Ca-Mg)-nitrate or of the German K-Mg-sulphates?

D. MULDER: In the case of successful soil application of manganese sulphate the soil was a fluvio-glacial sand of a pH of about 6.5, which was rather low in organic matter.

The amount of bitter-pit can be influenced in certain cases and under certain conditions by spraying with borax according to VAN STUIVENBERG. We found that in most cases the amount of bitter-pit is enlarged by spraying with borax.

According to VAN STUIVENBERG there should be a moment in the development of the apple at which spraying is successful. Water only controls were not included.

The symptoms of manganese deficiency appear both on young and older trees.

We made use of K-Mg-sulphates for fertilizing in case of magnesium deficiency.

T. S. SADASIVAN (Madras)

The Role of Trace Elements in Control of Root-Infecting Fungi

This paper discusses results of investigations on the response of three species of *Fusarium*—*F. vasinfectum*, *F. udum* and *F. moniliforme*—producing wilt on cotton, red-gram and paddy, respectively, both in pure culture and soil environment.

All the three species of *Fusarium* produced increased dry and ash weights in the presence of traces of boron, manganese and zinc when added to Richard's nutritive medium over their control. Higher ash weights with zinc and higher dry-weights with boron were recorded for all three fungi and it was shown that the former was due to inorganic salt accumulation and the latter due to carbohydrate accumulation. Interesting observations are included on potassium absorption and accumulation and sucrose consumption by the three fungi which, as indicated above, were greater in plus zinc cultures and plus boron cultures respectively.

Evidence is presented to show that addition of trace elements, particularly manganese at 40 p. p. m., in pot culture experiments controlled *Fusarium udum* disease of the red-gram plant; nevertheless, it had no ill effects on the host but induced earlier flowering, better seed-weight and generally increased plant vigour over the control.

The saprophytic activity of this fungus also diminished when "wilt-sick" soils were amended with boron, zinc or manganese. Even colonization of *F. udum* on plant debris from such soils was minimised.

Results of trace elements other than boron, zinc and manganese, viz., nickel, molybdenum, vanadium, aluminium, lithium, uranium, thorium, cobalt, rubidium and cadmium showed varying inhibitions on the micro- and macro-conidial production by *F. vasinfectum*, the most efficient of these being lithium. Similar results are presented on the inhibition of saprophytic activity of this fungus, the most

efficient trace element being boron. Another aspect discussed here is the effect of eight trace elements on stimulation of bacterial numbers in soils and its correlation with saprophytic activity of *Fusaria* in general; of particular advantage was the addition of boron which increased bacterial numbers to almost the efficiency of manganese yet combined the advantageous factor of higher toxicity on *F. vasinfectum* sporulation.

The addition of the micro-elements manganese, zinc and boron to natural wilt-sick soils maintained at pH 4.0, 5.0, 6.0, 7.0 and 8.0 in the laboratory brings about an increase in the total microbial population over the control at pH 7.0 and 8.0 in all the amendments; at pH 5.0 and 6.0 the population is lower than the control in plus manganese treatment alone, whereas plus boron treatment increases the population, and no significant increase or decrease is noticed in plus zinc treatment. At pH 4.0 manganese and zinc show no significant increase in micro-population in the various concentrations tried, whereas boron at lower concentrations shows lower micro-populations over the control, and further increase in concentration results in a positive correlation with increasing numbers, and at the highest concentration tried (400 p.p.m.) the largest population is at pH 4.0.

Discussion

D. J. D. NICHOLAS: In view of interesting effects of micronutrient elements on the composition of the microorganisms in soil, have you investigated the addition of these elements to soils at different pH levels?

T. S. SADASIVAN: The effect of pH on the host parasite relationship has been worked out over a large scale of pH from 5.0 to 8.5. There seems to be no great effect on colonisation or survival of the fungus *Fusarium vasinfectum*. However, the cotton plant responds well to growth only in the alkaline region. The question of immobilisation of some of the trace

elements, particularly molybdenum, is now being determined although preliminary work shows no great effect on the parasite.

OLOF SVANBERG (Uppsala)

Minor Elements in Pastures and their Relation to Animal Nutrition in Sweden

The interest within agriculture for botanical questions is to a rather great extent connected with the quality of the vegetation, judged by its effect as a food stuff on the yield of animal production.

From this point of view, the chemical composition of grass and legume crops, partly from ley farming, partly from permanent pastures, has attracted attention of agricultural science of our days.

The questions concerned are of outstanding interest for our understanding of the qualities of a favourable nutritional environment for animal husbandry, for the economy of animal breeding and consequently for the economy of agriculture as a whole.

The important influence of variations in the content of lime, and above all of phosphorus, in the crops used as fodder for highly producing domestic animals in our days are well known in all progressive countries. Besides the commonly well known macro elements, i.e. calcium, phosphorus, magnesium etc., a number of trace or minor elements has attracted attention for similar reasons during a number of years, in Sweden as in other countries. Altogether, these mineral nutrients for plants and animals may be defined as real ecological factors for crop production and for animal husbandry.

The author gives a brief review of Swedish experiences as to a number of trace elements in farming and feeding.

In Sweden, the vegetation from peat soils in the north of the country, and from sandy soils in the south, is generally found to be rather poor in *copper*. In all cases legumes are richer than grasses in this as in other metals. Clay soils, especially in middle Sweden, are

good sources for copper in the vegetation. In the case of *cobalt* a risk for shortage is nearly always prevalent if hay and pasture chiefly consist of grasses only, the risk however being accentuated on a number of peaty and sandy soils in all parts of the country.

On light sandy soils rich in lime, the *manganese* may drop in the vegetation to values really to low for dairy cows with a high milk production. Manganese, on the other hand, may be so abundantly represented in some uncultivated pastures as to make them quite inferior in quality, especially for horses.

D. J. D. NICHOLAS (Long Ashton, Bristol)
The Use of Aspergillus niger (Mulder's M strain) for the Determination of Mineral Nutrients in Soils and Plants

Microbiological methods for the determination of mineral nutrients in soil using fungi of the genus *Aspergillus* were introduced by Russian workers mainly for the determination of P in soils. SMITH and GOODWIN respectively have used the method for the assay of available P and K in British soils. STEINBERG has made a thorough investigation of the mineral requirements of *Aspergillus niger* under differential supply of C and S compounds. SMITH and MULDER have used the fungus to study available Mg and Cu in Dutch soils.

The method of bioassay proposed is based on the fact that the fungus will not complete its life cycle unless certain mineral nutrients are present in the culture medium, viz. macronutrients N, P, K, Mg and S, and micronutrients Fe, Zn, Cu, Mn, Mo and possibly Ga and V. Moreover, the response to the addition of an essential mineral element from deficiency to sufficiency levels, when others are present in adequate supply, is specific and quantitative. The standard growth series for an essential mineral element may be prepared by using as criteria the growth of mycelium, development of spores and dry weight yields of the fungus. For bioassay work a known amount of the

test material to be examined, viz. soil, extracts of fresh plant tissues, or the ash constituents of plants, is added to a standard culture solution containing all the mineral elements, other than the one to be determined. The growth of the fungus, under the condition of test, depends on the amount of the mineral nutrient it derives from the material added, and the test element may be assessed by reference to the prepared standards.

Special procedures for the purification of the mineral macronutrients and dextrose used in the culture solution are necessary for the bioassay of Mg, Cu, Zn, Fe, Mn and Mo respectively. The following nutrients may be removed from a solution of inorganic macronutrients and dextrose, as follows:

Magnesium: Recrystallisation or precipitation with 8-hydroxyquinoline at pH 8 (phosphates are omitted for the latter method of purification as they are precipitated in alkaline solution).

Iron: Extraction as a quinolate, using 8-hydroxyquinoline at pH 5, and after filtering, removing the iron quinolate and the residual quinoline with redistilled chloroform and ether.

Copper: Removal with dithizone in CCl_4 at pH 4 or co-precipitation with added Cu or Cd as a sulphide using H_2S . Elimination of H_2S by boiling.

Zinc: Extraction with dithizone in CCl_4 at pH 6 or extraction of quinolate in chloroform and ether using 8-hydroxyquinoline at pH 5.

Molybdenum: Co-precipitation of the metal with Fe or Al with 8-hydroxyquinoline at pH 5, or preferably as a sulphide in the presence of Cd, Cu and Pb using H_2S . The addition of I_2 in KI simultaneous with H_2S precipitation, facilitates the removal of further amounts of Mo, presumably due to the formation of colloidal S which acts as an additional collector of the element.

Manganese: Using sodium diethyl-dithio-carbamate and removing the manganese complex in CCl_4 . Excess organic reagent is removed

by the addition of Cu and excess Cu is removed by precipitating as a sulphide with H_2S .

In all instances, the mineral macronutrients and dextrose purified as described are used for the nutrient cultures and the micronutrients are added later. Following this procedure any phytocidal effects that may result from the addition of purifying reagents can be observed. Mineral micronutrients (AR) for test are recrystallised from glass distilled water using redistilled alcohol to enhance yields. It is advantageous to check their purity with a spectrograph before use.

Using the above methods satisfactory growth curves are obtained for the following mineral nutrients, as mg per 50 ml culture solution: Mg, 25 to 500; Cu, 0.05 to 2; Zn, 0.1 to 5; Fe, 0.01 to 5; Mn 0.01 to 2; Mo, 0.0001 to 0.02. The bioassay method applied to soil problems has shown: Mg deficiency in the presence of K deficiency, a point not shown by the chemical analysis of crop plants; Cu deficiency in alkaline fen soils where cereal crops were affected and sandy soils where fruit trees showed dieback symptoms; Zn deficiency in soils where apple, pear and other fruit trees showed "little leaf" effects; Mo deficiency in acid soils where brassica crops exhibited "whiptail" symptoms; and Mn deficiency in soils where farm and vegetable crops show the deficiency.

Because of the extreme sensitivity of the method, especially for Mo, it has been used to determine micronutrient levels in extracts of fresh plant tissues and in the ash of plants.

Little is known of the rôle of the micronutrients in the metabolism of the fungus. Molybdenum is required for the reduction of nitrate N to ammonia N, as is shown by the fact that its requirement for Mo is considerably reduced when urea N or ammonium N is the only source of nitrogen. Moreover, in the absence of Mo, when nitrate N is the sole source of nitrogen, nitrate N accumulated in the fungus and little amino N was detected, viz. trace of glutamic acid only. With increas-

ing amounts of Mo however, the nitrate N fraction decreased and the free amino N increased in the fungus indicating that nitrogen metabolism was proceeding more normally.

Vitamin B₁₂ is produced by the fungus but in media rigorously free from Co, the vitamin was not detected. The growth of the fungus, however, was not adversely affected by the absence of cobalt.

Discussion

OLOF SVANBERG: We are in this country highly interested in the questions concerning the minor elements from the points of view of crop production and animal husbandry. We are, however, working with chemical and spectroanalytical methods, and in most cases it is quite possible to attack our problems in this way, especially Mg giving good results. The most difficult and time-consuming methods concern the cobalt as a result of the really

very small quantities of this metal in the plant kingdom. It should be of great interest to know if Dr. NICHOLAS has something to tell us about possibilities for determination of cobalt with biological methods. We know that cobalt is essential for the growth of yeast, at least for some pedigrees of it, but how is the situation in respect to cobalt and *Aspergillus*?

D. J. D. NICHOLAS: As mentioned previously, the production of vitamin B₁₂ by *A. niger* is markedly reduced by a deficiency of cobalt in the diet. Moreover graded additions of the metal to media that had been rigorously freed from the element (quinoline purification procedure as for Fe) increased the amount of the vitamin produced but the dry weight yields of the fungus were unchanged. Thus a measurement of vitamin B₁₂ production by the fungus may provide a method for the assay of cobalt in biological materials. We are exploring this possibility.

SESSION 10 A

July 20th, 9 a. m. — 1 p. m., Attendance: 60 members

Chairman: F. T. WAHLEN, Recorder: E. ÅKERBERG

SUBJECT:

Plant Breeding

WILHELM RUDORF (Voldagsen/Elze)

Inbreeding and Heterosis with Helianthus annuus L.

1. The sunflower is chiefly insect pollinated. By structure and function of the flower, self pollination is nearly excluded.

2. 144 inbred lines from 3 Russian varieties have been obtained by repeated self pollination since 1939. After first isolation self-fertility varied from 1-82%. Inbred lines with normal fertility on self pollination have been obtained after elimination of the \pm self-sterile lines in 4-5 generations.

Exception: inbreds with abnormal flower heads.

3. Progressive homozygosity was observed at first, as known from other objects, by chlorophyll defects, dwarfs and numerous morphologic deformations, in higher generations by uniformity of the inbreds with regard to all morphological and physiological characteristics.

4. Inbreeding only has revealed the many-fold forms in sunflower. Depression by inbreeding varied highly from nearly non-viable to very vital inbreds with nearly no depression. Some dwarf lines are very vital and

Crossing of inbreds with the following characteristics	F ₁ dominant characteristics	F ₂ segregation numbers	Remarks of the genetic basis of characteristics
6 a. Chlorotic × normal green	Normal green	Chlorotic : normal green 69 : 316 $\chi^2 = 10,3$	"Chlorotic" monomere recessive. Chlorotic, less viable plants had died in part until classification.
b. Dwarf × high growing	High growing	Dwarf : medium high : high 64 : 621 : 119 146 : 394 : 305	Polyfactorial
Dwarf × dwarf	Recessive	89 dwarfs only	
c. Thin stalks of heads smoothly curved × thick stalks broadened and flattened beneath the heads and sharply bent down	Sharply bent down	Smoothly curved : sharply bent down 68 : 381 95 : 498	In F ₂ the recessive type was clearly recognized, besides several intermediate types which could not be grouped.
d. Branched × not branched	Not branched	Branched : not branched 121 : 570 54 : 110	In two inhomogeneous populations "branched" is recessive. Polyfactorial.
e. Small flower heads × big heads	Big heads	Heads small : medium : big 69 : 238 : 113	Polyfactorial
Small × medium heads	Medium heads	26 : 104 :	Polyfactorial

show high yields in grain. On the other hand high growing lines may have only small flower-heads and low yield.

5. Inbreds of different pedigree and differentiated characteristics were crossed. Self pollination of the mother plants could not be avoided: In F₁, plants from cross pollination are recognizable by heterosis and dominance of paternal characteristics. Plants from self pollination were eliminated. Heterosis manifested itself by increased growing capacity and luxury of certain organs. Elongation of the stems in F₁ ascended to 9–60 % compared with the ♀ inbreds, and to 1–74 % compared with the ♂ inbreds. Increase of thickness of the stems in F₁: 30–130 % and 24–123 % resp.; increase of diameter of the flower heads in F₁: 11–86 % and 24–84 % resp.

6. The heredity of several characteristics was studied in F₂-populations. See table.

7. The observations on inbreeding and het-

erosis with *Helianthus annuus* agree completely with those made with maize. They support the hypothesis that heterosis is caused by addition effects of dominant alleles and can therefore be fixed genetically.

8. These studies were made in the course of breeding sunflower varieties, adapted to German climatic conditions. Utilization of hybrid vigor is practised in Canada and southern Russia where climatic conditions are favourable for insect pollination.

Discussion

F. T. WAHLEN: War das heterotische Zuchtmaterial gross genug für die quantitative Erfassung der Leistungsmerkmale, insbesondere des Ölertrags?

Sind Formen aufgetreten, die sich besonders als Silagepflanzen eignen würden?

R. BOUILLENNE (Liège)

La Sexualisation du Fraisier des quatre saisons à fruits rouges

Le développement du Fraisier des quatre saisons à fruits rouges est marqué par des changements continus dans les activités foliaires du méristème de la tige. Les feuilles successives sont de plus en plus compliquées, d'abord monofoliées, puis bifoliées, puis trifoliées; leur dentelure et leur nervation sont progressivement plus abondantes.

Lorsque les bords du limbe des dernières feuilles sont découpées par plus d'une cinquantaine de dents environ, on peut affirmer que la plante va fleurir. Après la sexualisation, la dentelure ne dépasse jamais le niveau de 60 dents.

La forme des feuilles donne d'excellentes indications sur l'état de développement du méristème qui les édifie; on peut établir aisément par ce moyen qu'une plante est dans un état plus ou moins proche de sa floraison.

Le développement normal du Fraisier des quatre saisons a lieu en jours longs. En jours courts, (8 ou 10 h.) la plante se développe anormalement.

Par exemple, lorsque les jours courts sont appliqués à partir du semis, la dentelure des feuilles se complique plus lentement de feuille à feuille, qu'elle ne le fait en jours normaux; de plus, la complication de la dentelure atteint au maximum 50 dents; la plante ne fleurit pas.

Lorsque les jours courts sont appliqués, non à partir du semis, mais sur une plante dont le développement est fort avancé, (les dernières feuilles ayant par exemple de 40 à 45 dents), et qui s'est développée jusque-là en jours longs, les nouvelles feuilles, formées en jours courts, sont progressivement très compliquées et leur dentelure peut atteindre jusqu'à 80 dents, ce qui ne se produit jamais à l'état normal. Il n'y a pas de floraison.

Ainsi, l'application de jours courts a deux effets simultanés: elle empêche la floraison et

affecte la forme des feuilles. On constate que la courbe relatant l'évolution du nombre de dents de feuille à feuille, renseigne parfaitement sur les qualités du développement de la plante, cette courbe a une allure différente selon que le développement est normal (jours longs) ou anormal (jours courts).

Lorsque le développement est normal, la coloration verte des limbes étalés est sombre, tandis que lorsqu'il est anormal, elle est beaucoup plus claire. Si on saponifie à la potasse alcoolique pendant 48 heures un lambeau de limbe d'une feuille étalée depuis un certain temps et qui a largement achevé sa croissance, les cellules de parenchyme en palissade du limbe, contiennent, après ce traitement, de grosses gouttelettes de couleur jaune à la condition que le développement de la plante ait lieu en jours longs et soit normal. Par contre, si le développement de la plante est anormal, donc en jours courts, la saponification à la potasse alcoolique pendant 48 h. fait apparaître, dans les mêmes cellules, des cristaux de caroténoïdes rouges. On peut affirmer que l'insaponifiable est de qualité différente selon qu'il s'agit d'un développement normal (jours longs) ou d'un développement anormal (jours courts).

Des observations analogues peuvent être faites de la manière suivante: le Fraisier émet constamment des stolons. Lorsque la plante est en fleur, les plantes qui se forment le long de ses stolons fleurissent très rapidement, à condition qu'ils soient en contact par le filet avec la plante-mère. La saponification révèle, chez ces plantes, la présence de gouttelettes jaunes dans les cellules du parenchyme des limbes.

Si on coupe le filet, on peut obtenir des plantes isolées de leur plante-mère et qui ne fleurissent pas. Dans ce cas, la saponification ne révèle plus la présence de gouttelettes jaunes dans les limbes; on y trouve de cristaux brunrouges.

Il est cependant possible de faire fleurir ces plantes isolées en appliquant sur les limbes et les pétioles de leurs feuilles étalées, l'extrait insaponifiable brut obtenu à partir de feuilles

adultes appartenant à des plantes dont le développement est normal, par exemple à des plantes sexuées, en fleurs, cultivées en jours longs. Cet extrait insaponifiable est une huile jaune très complexe. On démontre ainsi que l'insaponifiable des feuilles de ces plantes contient des substances favorables à la floraison.

Discussion

R. BAUER: In Germany (Voldagsen) I found in variety-trials, planted in American "Double spaced row-system", one variety named "Moulin rouge," which flowers and fruits also under long-day conditions in the stolon-plants.

INGVAR GRANHALL (Balsgård, Sweden) *Frost Resistance Problems in Fruit Tree Breeding*

On account of the severe winter climate in Sweden, and especially the low temperatures during the rest period of the fruit trees in January–February, the hardiness is a very important varietal character. The present assortment has, however, many weak points, and extensive breeding work is therefore taken up at the Balsgård Fruit Breeding Institute since 1942.

The Institute is now equipped with a good artificial freezing laboratory and investigations have been carried out during two winters in order to find an agreeable hardiness selection method. Exposing branches and twigs of apple and other fruit trees to -30 to -40°C during 24–48 hours in January–February gave results surprisingly parallel to the hardiness ranking of market varieties based upon field observations after the severe winters in the early forties. The hardest apple group, A, of these freezing trials comprised Russian, Baltic and Swedish varieties, *e.g.* Antonovka, Charlamovsky, Hibernat, Slava Petersburg, Transparente Blanche, and Åkerö. The second group, B, contained, *inter alia*, the North American varieties Lobo, Mc Intosh, Melba, Milton and Wealthy. The majority of varieties

fell into the middle-grade and sensitive groups C, D, E.

About one hundred new apple selections with promising records in other characters have been tested in the freezing trials of last winter. The best average result showed the cross Guldberg (group B) \times Transparente Blanche (group A) with five tested descendants all classified in groups AB. In other cases transgressions occurred, *e.g.* Ontario (D) \times Filippa (C) presenting three plants in AB. The triploid Ribston (C) has also given a comparatively good diploid progeny after open pollination, 12 out of 26 ranking in groups AB.

In the winter 1948–49 31 tetraploids were frozen, and in 1949–50 the number was 38, 24 of which were tested for the second time. The cold resistance of the tetraploids showed a wide range of variation from B to E. The triploid mother varieties were all middle grade (Ribston: C) or sensitive (Belle de Boskoop, Canada Reinette, Vram's Iron apple, Gallo-way, Mère de Ménage: DE). The best tetraploids belonged to the Ribston family, 3 out of 13 being assigned to group B. It seems evident that the polyploidy *per se* does not decide the hardiness. In the breeding program crosses between diploids and tetraploids are extensively used, and of course the hardest tetraploids are very valuable in these combinations.

The combining of tree hardiness with late ripening and long storage capacity of the fruits is often a difficult task on account of the delayed winter maturing of the tree tissues accompanied by autumn frost sensibility. Spring frosts at apple blossom can be avoided by breeding late flowering varieties, *e.g.* from combinations with Hans Mathiesen, Crawley Beauty and Court Pendu Plat.

Frost resistance breeding is placed in the foreground also in pears, plums, cherries, hazelnuts and rootstocks.

Discussion

W. RUDOLF: I might ask Dr. GRANHALL if he has observed a correlation between winter-

hardiness and late time of leaf dropping in the autumn and whether he could find among his varieties some that combine late time of leaf dropping with late time of ripening?

I. GRANHALL: Correlation between early leaf drop and hardiness seems to be the rule. Some varieties in the assortment at Balsgård are late ripening and at the same time hardy. It must, however, be emphasized that the time table of maturing and leaf drop can be very different in different climatic regions.

J. M. POEHLMAN (Columbia, Mo.)

Breeding Winter Barleys for Hardiness and Disease Resistance

The merits of winter barley make it an important crop in the development of a diversified agriculture in the southern United States. In the state of Missouri, winter barley needs to be made a safer crop for the farmer to grow, if its acreage is to be expanded and extended northward. Safety may be achieved by the use of good production practices, liberal use of balanced fertilizers, and improvement in the inherent winter hardiness and disease resistance of the varieties being grown. Possibilities of the latter are discussed here.

Three procedures for breeding more hardy strains are suggested. These are: (1) finding and introducing a more hardy variety, (2) crossing hardy varieties of diverse origin to obtain transgressive improvement, and (3) increasing resistance to diseases which infect and weaken fall-seeded barleys. Many barley varieties from the United States Department of Agriculture World Collection have been tested, but introduced strains more hardy than the Tennessee winter type varieties already grown have not been found. Until more hardy parent material is uncovered, increasing hardiness by transgressive improvement must necessarily be a slow procedure. The possibility of reducing winter injury by developing strains resistant to the common diseases which infect and weaken the barley plants in the fall, thereby leaving them more vulnerable to the

rigors of cold and heaving, offers an immediate approach to the problem, although heretofore it has been given little attention.

Sources of disease resistance are commonly known in the spring-type barley varieties, but information about the winter-type has been rather meager. If the best combinations of hardiness and disease resistance are to be obtained, relatively hardy varieties should be available as sources of the disease resistance. To find these varieties a careful survey of disease resistance in hardy, winter-type varieties has been conducted. It was learned that resistance to scald (*Rhynchosporium secalis*) is carried by many rough-awned Tennessee winter type varieties. Many of the Tennessee hooded-type varieties are resistant to the loose smuts (*Ustilago nuda* and *U. nigra*). Resistance to mildew (*Erysiphe graminis, hordei*) and one or more of the three smut diseases was found in introductions from Chosen, China, and the Caucasus area. Selections from crosses between the rough-awned and hooded Tennessee types have exhibited resistance to fall infections of spot-blotch (*Helminthosporium sativum*). Studies are now going forward to determine resistance of selected strains to individual physiologic races of the smut diseases. Crosses have already been made to combine resistance to several diseases into single strains.

Discussion

I. GRANHALL: In the breeding of winter barley at Svalöf, of which I was in charge some years ago, we found that there were no really hardy varieties to compare with e.g. our best wheats. By means of transgression breeding it was, however, possible to find new types with excellent hardiness, and I can mention that several astonishingly good lines were obtained from crosses between Central European "Wechselgerste" and Swedish spring barley, both parents being very sensitive. The heaving problem is, however, very severe in certain soils. Mildew resistance and straw strength are also insufficient.

F. R. HORNE: Preliminary trials in Britain indicate that mildew resistant varieties of spring oats from the Welsh Plant Breeding Station gave increases in yield up to fifteen per cent over the susceptible control variety in seasons when mildew is severe.

Agronomic observations at the National Institute of Agriculture Botany, Cambridge, suggest that loose smut under certain conditions may not cause serious reduction in yield; this is possibly due to compensating growth made by other tillers on the same or adjoining plants.

J. M. POEHLMAN: In answer to Dr. HORNE's question regarding assessment of amount of damage due to mildew:

We have not made an accurate assessment of damage by mildew in Missouri since infections are erratic and depend upon the seasonal conditions. Further east along the Atlantic coast where mildew is more serious, I believe it is estimated that loss may run from 5 to 15 per cent.

In answer to Dr. HORNE's question regarding the effects of the different strains of smut on the plant:

We have until the last three years been working with a single collection of the loose smut organism, *Ustilago nuda*, but with our

recent studies of collections have noted that strains of smut differ not only in their virulence but also in their effects on the plant such as reduction of tillering, etc.

HUGO OSVALD: In recent years we have tried to introduce winter barley in Swedish farming practice. We have, of course, mainly used the variety bred by Dr. GRANHALL. The varieties available in Sweden are, however, not hardy enough in Middle Sweden, and they are not resistant to diseases. We are therefore looking for new varieties. I should like to ask prof. POEHLMAN if there are many of his strains that are resistant to two of the diseases. I should also like to ask whether it might be possible to obtain some of the best of prof. POEHLMAN's strains for testing at the Royal Agricultural College in Sweden.

J. M. POEHLMAN: On answer to Dr. OSVALD's question as to whether resistance to more than one disease has been found in a single variety:

The Tennessee hooded varieties frequently combine resistance to *Ustilago nigra* with resistance to *Ustilago nuda* and one strain combines resistance to all three smuts.

Resistance to the three smuts and to mildew are combined in some of the strains from Chosen or Korea.

SESSION 10 B

July 20th, after 10 A, Attendance: 60 members

Chairman: F. T. WAHLEN, Recorder: E. ÅKERBERG

SUBJECT:

Phytopathology

T. GOODEY (Harpenden, Herts.)

Oats and Varietal Susceptibility to Stem Eelworm Infestation

In Britain the stem eelworm, *Ditylenchus dipsaci*, causes a disease of oats characterized by severe stunting of the seedling with thicken-

ing of the ensheathing leaf bases which become soft and discoloured. The same race of the eelworm will also attack onions, field beans, parsnips, mangolds and rhubarb as well as the following weeds: *Stellaria media* (L.) Vill., *Polygonum Convolvulus* L., *Anagallis arvensis* L., *Cerastium vulgatum* L., and

Arenaria serpyllifolia L., which serve as reservoir hosts.

Crop losses due to eelworm could be avoided by the use of oat varieties resistant to eelworm infestation. A few such are known and are winter varieties, the chief one being Grey Winter. Avoine d'hiver and the white-grained Unique are also resistant. The hybrid, S. 81 (Grey Winter \times Kyko) is resistant but a selection from the same cross, S. 82 is very susceptible, Picton (Grey Winter \times Argentine) though showing promise of resistance some years ago is now reported susceptible. A resistant spring oat is much needed but more than 40 tested by the writer during the past 17 years have all proved susceptible.

In California, THOMAS in 1939 reported that out of 130 oat varieties tested for susceptibility to stem eelworm, only three, Capa, Pampa and Victoria, were resistant. In 1940 the writer tested these three varieties in England and found them resistant. One naturally asked could these varieties be used for breeding purposes to get the quality of eelworm resistance into a spring oat?

E. T. JONES, the oat breeder of Aberystwyth, in correspondence, agreed that all three could be so used but pointed out that owing to their inferior agricultural qualities the use of Capa and Pampa would render the raising of a good resistant hybrid a slow business. An objection to using Victoria is that it has been found in U. S. A. wholly susceptible to a fungal disease due to *Helminthosporium victoriae*. This susceptibility is linked to resistance to crown rust. If this quality were also found to be firmly linked to eelworm resistance, Victoria could not be used. Grey Winter, however, might be used and back-crossed with a spring type provided there is no link between winter hardiness and resistance to stem eelworm.

Discussion

E. VAN SLOTEREN: You did say that the oats eelworm attacked onions, among others.

Do you know whether this eelworm of oats is identical with the eelworm that attacks onions everywhere in the continent of Europe? Our experience is that the finding of a certain eelworm in a crop does not prove its identity with the eelworm that is a regular habitant of this crop.

T. GOODEY: Experiments have shown that the stem eelworm from teasel, rye, oats, man-golds, beans, red clover, lucerne, and narcissus, as well as from the weeds already mentioned, can infest and reproduce in onion seedlings but this really proves nothing. *Ditylenchus dipsaci* from all these hosts are morphologically indistinguishable from one another but though all of them will infest and reproduce in onion seedlings they are not biologically identical. For example, though *D. dipsaci* from narcissus bulbs will infest and destroy onion seedlings, *D. dipsaci* causing typical "bloat" of onions will not infest narcissus bulbs or leaves. Again, the two biological races of the parasite infesting red clover and lucerne, though capable of invading onion seedlings do not attack oats and rye. *D. dipsaci* from teasel, rye and oats, though capable of invading seedlings of red clover and lucerne will not reproduce in them with the production of typical disease symptoms. I thus agree with Prof. v. SLOTEREN that the finding of *D. dipsaci* in various plants does not prove that the parasite is biologically one and the same.

J. TH. W. MONTAGNE (Amsterdam)

Soil Fumigation for the Control of Plant Diseases and Conditions Affecting the Results

Soil-borne pests and diseases are in most agricultural areas of increasing economic importance. In the past in many cases efforts to control these problems have been unsuccessful. Next to the search for resistant or tolerant plant varieties, soil fumigation is one of the more promising methods to tackle this prob-

lem. The application of a volatile toxicant in liquid form at a depth of 6–8 inches may result in a partial sterilisation of a zone of a foot or more deep.

The success of such a soil fumigation, however, is dependent on soil factors such as type of soil, structure, pH, degree of saturation of the moisture equivalent, temperature, etc. The optimal conditions for a successful application are different for each soil fumigant.

The location of the parasite to be controlled is very important. Surface-borne micro-organisms (e.g. damping off) cannot be controlled with a normal fumigation by injection at 6 inches depth. Other techniques such as sealing of the soil after fumigation, application of a soil-drench, mixing the soil surface with a solid fumigant are more successful.

The stage of the parasite to be controlled requires special attention. Sclerotia of fungi, cysts of nematodes, dormant stages of parasites located in non-decayed plant rests are more resistant than the free-living stages of the parasites.

In the experiments described in this paper special attention was paid to the rôle of water in connection with the results of a fumigation. An excess of water in the soil prevents the penetration of the volatile fumigant in the soil. However, water increases the sensitivity of many resistant stages of the parasites towards the toxicants. On the other hand water can be used as a carrier for the toxicants. A soil treatment with adequate emulsions of a toxicant like chloro-bromo-propene or DD gave a better killing of sclerotial bodies or cysts of *Heterodera Schachtii* than the same amount of the toxicants applied as such.

Fumigants like DD, chloro-bromo-propene, chloropicrin and EDB are all too toxic for normal applications in the presence of most living plants.

Low dosages of DD and chloro-bromo-propene emulsified in water are far less phytotoxic and offer the possibility of treating living plants, e.g. various fruit trees and other perennials.

M. PLAUT (Rehovot)

Die Anwendung von Aethylendibromid als Schutzmittel für die Aufbewahrung von Saat und Getreide

Aethylendibromid wurde versuchsmässig 1925 auf seine Wirkung auf *Tribolium* und *Sitotroga* untersucht. (U. S. A.; Bulletin 1303 Washington, NEUFERT et al.). Die ausserordentliche Wirkung wurde damals nicht erkannt, da die spezifischen Eigenschaften des Aethylendibromid (Siedepunkt 129°) infolge dessen langsame Flüchtigkeit nicht berücksichtigt wurden. NEUFERT et al. schreiben: "Ethylen-dibromide and Ethylbromide are the only bromides which have seen a further trial" (p. 13).

Die Anwendung von Areginal (I. G. Farben) (Halogenide der Kohlenwasserstoffe) veranlasste mich nach anderen Halogeniden und insbesondere Bromiden zu suchen, die für den Middle East in Frage kommen, zumal da Israel einer der Hauptproduzenten der Welt für Brom ist.

Veranlasst wurden die Versuche durch die Schwierigkeit Saat von *Vigna sinensis* (Cowpea) ohne schwere Verluste durch Käferfrass, *Bruchus*, aufzuheben. Nach anfänglichen Schwierigkeiten der Methode und Zeit der Anwendung fanden wir in Gemeinschaft mit den Mitarbeitern MASO, Agricultural Research Station, und AMAN et al., Physikalisch-chemische Abteilung der Hebrew University, in den Versuchen 1942, dass in Aethylendibromid bei entsprechender Zeit und Konzentration, die nicht zu hoch sein darf, eines der besten, erfolgreichsten und bequemsten Mittel zur Vergasung von Getreide und Leguminosen-Saat vorliegt, worüber der Palestine War Supply Board Scientific Advisory Committee 1943/44 berichtet hat (submitted by the Middle East Supply Centre, Government Printer, Jerusalem).

Im Vergleich zu HCN hat Aethylendibromid, wie wir es anwenden, folgende Vorteile:

- 1) Es ist viel weniger toxisch für Menschen.
- 2) Es kann von Personal ohne besondere Vorbildung angewandt werden.

3) Es ist unlöslich in Wasser und wird nicht leicht von Nahrungsmitteln absorbiert.

4) Es kann im Middle East und besonders in Israel aus heimischen Rohstoffen hergestellt werden.

5) Die Menge der Anwendung pro Tonne ist viel kleiner (ca. 1/8) als die Mischung von Aethylendichlorid und Kohlenstofftetrachlorid.

Die Resultate wurden nach dem Stand 1942 und 1946 in den *Annals of Applied Biology*, Cambridge University Press, 1946, Vol. 33 No. 4, p. 389–396 veröffentlicht. (The use of Aethylendibromid as a fumigant for grain and seed.)

Seit 1942 bis 1950 haben wir und die landwirtschaftlichen Kooperativen in Israel (KWuzot) und die private Landwirtschaft Aethylendibromid als hauptsächliches Vergasungs-Mittel für Getreidesilos, Lagerräume, für Saaten, in geschlossenen Eisenfässern, für Bienen, auch für Herbarzwecke angewandt. Im Gegensatz zu den bekannten zahllosen Mischungen von Aethylendibromid, die von der amerikanischen Firma Dow seit 1946 empfohlen werden (auch von Thompson-Hayward Chemical Co. Kansas 5% und 15% Aethylendibromid-Mischungen) wenden wir seit 1942 Aethylendibromid unverdünnt ununterbrochen an; Keimschädigungen und Gesundheitsschäden sind uns nicht bekannt geworden. (Sowohl nach früheren, wie neuen Versuchen.) Ob Aethylendibromid bei derselben Saat mehrmals angewendet werden kann, ist eine Frage die immer wieder auftaucht. Es scheint uns wahrscheinlich. Aethylendibromid bei Mehl und Nudeln für kleine Mengen angewandt mit nachfolgender Lüftung, gibt keinen merklichen und schädlichen Einfluss.

Von den Bienenzüchtern wird jetzt auch in größerem Umfang Aethylendibromid angewendet und hat sich gegenüber der früheren Schwefelung bewährt.

Wir benutzen heute bei Saaten Aethylendibromid bei Tages-Mitteltemperaturen

25–35°	3 Tage
18–25	5 Tage
12–18	7 Tage bei 50–75 g (ca. 30 cm ³)/m ³ .

Für Getreidesilos lassen wir in den Kopf des Elevators Aethylendibromid langsam aus einem Petrol-Behälter mit Hahn eintropfen. In allen Lagerräumen werden kleine Vergasungs-Kammern für Getreide- und Korn-Muster und Säcke eingebaut. Das Mittel ist billig, pro Kilogramm ca. 1 LP, also pro Tonne Getreide ca. 1 1/2–2 sh.

Neuerdings wird Aethylendibromid auch gegen Nemathoden und Bodenvergasung verwendet, auch für die schwierige Aufbewahrung und Kultur von Bataten wird es neuerdings in Amerika empfohlen.

Der allgemeinen Anwendung von Aethylendibromid für die verschiedensten Zwecke steht nach unseren Erfahrungen nichts im Wege.

Discussion

H. MELCHIOR: Wie ist die Wirkung von Aethylidibromid auf Milben und besteht eine Einwirkung auf den Menschen?

MENKO PLAUT: Entomologists' experiments have not shown that ethylene dibromide also kills *Acarinae*. It is less dangerous for men than other insecticides, and much less so than methyle bromide. Ethylene dibromide is used in Israel in all farms with good results. It is used also in U. S. A. against nematodes as a soil fumigant.

M. B. HYDE (Slough, Bucks.)

The Occurrence and Significance of Sub-Epidermal Fungi in Cereal Grains

The suggestion of various workers that micro-organisms may be responsible for some of the deterioration of damp grain during storage has been confirmed by work at the Pest Infestation Laboratory, in which it was shown that the respiration of insect-free wheat, which increased during storage without any morphological change in the seed, could be reduced if the bran coat, together with a sub-epidermal mycelium which was shown to be present beneath it, was removed by abrasion.

The sub-epidermal fungus in wheat, which is now being investigated in further detail, is present as a branched, septate mycelium extending over the inner surface of the epidermis, the hyphae occurring more abundantly in the regions where the epidermis is free from the underlying layers of the pericarp.

The fungi, generally present in a vegetative condition only, have been provisionally identified from cultures from surface-sterilized grain as non-pathogenic species, *Alternaria tenuis* occurring most commonly, and *Cladosporium herbarum* and species of *Fusarium* and *Stemphylium* less frequently.

A survey of normal crops from most of the wheat-producing areas of the world has shown that the amount of sub-epidermal mycelium, which is universal in distribution, and absent only from a few localities where wheat is grown under irrigation, appears to be related more to climatic conditions, particularly atmospheric humidity in the two to three weeks before harvest, than to variety or type of wheat, etc.

It is at this late stage of development, when the glumes have opened to expose the grains, which have reached full dry weight and have dried out to a moisture content of 30 to 35 %, that the internal mycelium is first seen. It is suggested that it arises from chance air-borne spores and external hyphae already present on the dead stamen and stigma remains, and not from an up-growing systemic infection as in a similarly situated mycelium in *Lolium* spp., but actual penetration of the one-celled epidermis has not yet been seen.

Attempts to grow wheat to maturity under sterile conditions, to obtain grain free from internal fungus for comparison with normal grains, have been unsuccessful.

The virtually fungus-free wheat from very dry areas suggested that wheat grown under simulated irrigation conditions might be free from internal mycelium, and a technique of enclosing ears singly or in pairs in flasks containing a desiccant at quite a late stage of development has been found to be completely

successful in producing fungus-free grain of normal weight, viability, etc.

Spraying individual ears with fungicidal or fungistatic substances, notably 8-hydroxyquinoline sulphate, also resulted in fungus-free grain.

Both these methods are too laborious for use on anything but a laboratory scale, but can produce amounts of fungus-free grain sufficient for respiration studies, for which a conductometric method for measuring carbon dioxide, accurate to 1 microgram, has been developed.

This investigation is still in progress, and respiration measurements on this year's crop should make it possible to obtain more information on the importance of these sub-epidermal fungi in the physiological behaviour of stored wheat.

Discussion

J. M. POEHLMAN: Do you find combine-harvested wheat to be more heavily infected than binder-harvested wheat?

F. R. HORNE: The observation that fungi are present in samples of wheat from all but the very dry areas and that all grains in the sample are usually infected is of great interest from the point of view of germination behaviour in seed stocks of wheat. Their presence may determine the behaviour of seeds when subjected to slow germination due to low soil temperature when poor growth under field conditions is noted.

It would also be valuable to compare the extent of infection in samples of wheat from low rainfall and high rainfall areas respectively as this might indicate why the former areas frequently supply seed giving the higher establishments in the field.

A. MACLEOD: Fungi under the husk in barley which produce mucilage are responsible for enhancing dormancy in barley. This dormancy is more prevalent in wet harvests.

Was there any evidence of mucilage in the wheat grains with subepidermal fungi?

Did these fungi contribute to wheat dormancy?

M. B. HYDE:

1) The difference between combine-harvested and binder-harvested wheat has not been investigated, but it is possible that combined wheat, cut at an earlier stage and dried more rapidly than wheat which is reaped and stooked, would have less internal mycelium.

2) Germination at humidities likely to be found in the soil.—This had not been studied; experimental storage at high humidities did encourage heavier development of subepidermal fungi.

3) Difference in amount of fungus between East and West.—There was more fungus (about 3:2) in the West of England (Devon) than in the East (Cambridge), a region with less rainfall than the West.

4) Mucilage and its effect on germination.—This had not been investigated, but there did not seem to be much mucilage present.

5) Effect of the fungi on germination.—Germination was the same (98–100 %) in both normal (infected) and artificially produced fungus-free grain, when examined 10–14 days after harvest, so it was not thought that the fungi had produced dormancy in the grain.

BERTHA MOORE and MARTIN TVEIT
(Harpenden, Herts. and St. Paul, Minn.)
*Antibiotic Action of Chaetomium sp. on
Organisms Causing Root-Rot of Oats*

A species of *Chaetomium* was isolated from Brazilian-grown oats seed and was found to

be extremely antibiotic to some of the organisms causing root rot of oats. The strongest antibiotic action was against *Helminthosporium victoriae* on Vieland oats, which in the absence of any control is sufficiently pathogenic to kill all plants in the seedling stage. When a mycelial suspension of the *Chaetomium* sp. was added to the soil at the time of planting and in the same amount as inoculum of *H. victoriae*, a perfect stand of plants resulted which remained healthy to the end of the experiment when the plants were in the four to five-leaf stage. It was equally effective in sterile or non-sterile soil, and with artificially or naturally inoculated seed. The *Chaetomium* sp. is similarly antibiotic to *Helminthosporium avenae* and *Helminthosporium pedicellatum* both in culture and in soil; and somewhat less so to species of *Fusarium*, *Alternaria*, and *Rhizoctonia* in culture. It is strongly antibiotic to many bacteria in culture, and while not antibiotic to *Trichoderma* sp. and *Mucor* sp. it was not inhibited by these or by any of the other common fungi with which it was grown. It apparently protected flax seedlings from some of the soil-borne seedling disease organisms. The specific identity of the *Chaetomium* has not been determined, but it appears similar to *C. cochlioides* Palliser. Three culturally distinct types were isolated from the Brazilian-grown seed, which differ greatly in rate of growth and production of perithecia, but are equally antibiotic when equal amounts of mycelium are used. Somewhat similar isolates of *Chaetomium* from Minnesota-grown seed were not antibiotic.

CYTOLOGY, CYT

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SESSION 1

Jointly with Section GEN: July 12th, 2—4 p. m., See page 324

SESSION 2

July 14th, 9 a. m. — 1 p. m., Attendance: 50 members

Chairman: E. HEITZ, Recorder: A. LEVAN

SUBJECT:

Experimental Influences on Mitosis and Chromosomes

CORNELIA HARTE (Freiburg im Breisgau)

Die Wirkung von Meterwellen auf Zellkern und Chromosomen

Meterwellen kommen als Komponente der kosmischen Strahlung in der Natur vor und werden auch in Medizin und Technik vielfach verwendet. Es ist daher wichtig, ihre Wirkung auf biologische Objekte zu kennen. Für die Untersuchungen wurden Infloreszenzen von *Oenothera (suaveolens sulfurea × Hookeri) flava* verwendet, die mit einer Feldstärke von 1200 mV/m 15 Min. bis 12 Std. behandelt wurden. Die Knospen wurden dann nach 2, 4 und 6 Tagen fixiert. Bei einer Bestrahlung von 15 Min. finden sich nach 2 Tagen in den PMZ Störungen, die dem Primäreffekt nach Röntgenbestrahlung entsprechen. Nach 4 Tagen sind diese verschwunden, dafür lassen sich in grösserem Umfang neue Chromosomenanordnungen

in der Diakinese feststellen, die nur durch Chromosomenmutationen zu erklären sind. Diese betreffen meist Chromatiden, aber auch ganze Chromosomen, wie sich an den Fragmenten erkennen lässt. Bei längerer Behandlung verändert sich diese Wirkung nicht wesentlich. Ein geringer Anstieg in der Häufigkeit der aberranten Zellen nach Bestrahlung von 12 Std. ist statistisch nicht gesichert. Die Translokationen kommen zwischen Chromosomen, die bei der Paarung benachbart sind, häufiger vor als zwischen solchen verschiedener Paarungsgruppen. Die Restitutionen müssen also zu einem Zeitpunkt vor sich gehen, in dem die homologen Chromosomen einander bereits genähert sind, wahrscheinlich zu Beginn des Pachytäns, aber nicht im Ruhekerne.

An der Mitose von *Vicia Faba* konnte durch BRAUER am Anstieg der Mitosenhäufigkeit bei der Behandlung mit niedrigen Feldstärken eine

Förderung des Teilungswachstums gesichert werden, während bei grösseren Feldstärken eine Hemmung und Schädigung eintritt. Für die Beeinflussung der Mitose ist die Behandlungsdauer von grösserer Bedeutung als die Feldstärke, der die Pflanzen ausgesetzt sind, während für die mutationsauslösende Wirkung in der Meiose die Zeitdauer der Bestrahlung fast völlig gleichgültig ist. Die Reaktion hängt in beiden Fällen nicht mit der eingestrahnten Energiemenge zusammen. Bei den verwendeten niedrigen Feldstärken wäre eine Erklärung der mutagenen Wirkung durch Trefferereignisse nur schwer möglich, während durch die fehlende Energieabhängigkeit eine solche völlig unmöglich wird. Es kann also keine direkte Wirkung auf die Chromosomen vorliegen, sondern es muss angenommen werden, dass die Zelle als Ganzes von der Strahlung getroffen wird und darauf reagiert, wobei als erstes, bis jetzt feststellbares Ergebnis der Bruch der Chromosomen zu finden ist. Bei der Mutationsauslösung durch Meterwellen ist die Energieabsorption am Chromosom nicht der entscheidende Vorgang, sondern die mutagene Wirkung greift an einer anderen Stelle des Zellgefüges an. Über die zwischen diesem ersten Einfluss und dem endgültig abgelaufenen Bruch des Chromosoms liegenden Vorgänge ist bis jetzt noch keine Vermutung möglich.

Discussion

E. KNAPP: Die Häufigkeit der Mutationen kann wohl nur dann unabhängig von der eingestrahnten Energie sein, wenn ein gewisser Schwellenwert der Energie und der Feldstärke, die erforderlich sind, um eine bestimmte, zur Auslösung von Mutationen führende Änderung des Zustandes der Zelle herbeizuführen, überschritten ist. Ist dieser Grenzbereich der für die Auslösung von Mutationen erforderlichen Energiemenge und Feldstärke untersucht? Ist es bekannt, ob bei Feldstärken, wie sie in der Umgebung von Rundfunksendern u. dergl. Organismen treffen, mit der Auslösung von Mutationen oder Beeinflussungen der Zellteilungsvorgänge zu rechnen ist? Wie sind in

dieser Hinsicht die therapeutischen Anwendungen dieser Strahlenqualitäten zu beurteilen?

C. HARTE: Die Wirkung der Meterwellen kann sowohl eine Schwellenwert- wie eine Schockreaktion sein. Darüber können erst die in diesem Jahr zur Klärung dieser Frage bereits durchgeführten Versuche eine Antwort geben. Die Wirkung von Rundfunksendern auf die Pflanzen in ihrer Umgebung wird untersucht. Vor Beendigung der Untersuchungen kann ich über die Ergebnisse keine näheren Angaben machen.

JOE HIN TJIO (Zaragoza)

Chromosome Fragmentation by Pyrogallol in Vicia faba

The chromosome fragmentation induced by phenols in *Allium* (LEVAN and TJIO 1948) had been retested with more or less negative results by THERMAN-SUOMALAINEN (1949, in *Podophyllum*, *Pisum* and *Vicia sativa*) and by LOVELESS and REVELL (1949, in *Vicia faba*). It was therefore decided to test pyrogallol in another plant than *Allium*, viz. in *Vicia faba*, root tips being treated from 4 to 24 hours with aqueous solutions of pyrogallol in concentrations from 0.1 to 0.00001 mol/l.

The concentration zone 0.1–0.005 mol/l gave toxic effects, the turgor of the roots being lost within 24 hours. Pycnosis and mitosis inhibition occurred. C-mitotic effects were found in 0.02–0.002 mol/l. In the region 0.002–0.00005 mol/l radiomimetic effects were found. They were mainly of the primary type and consisted of free as well as attached fragments, chromosome erosions and a few pseudochiasmata. Chromosome breakages and erosions had their highest frequency at 0.005–0.0005 mol/l after 4 hours. As much as 10–15 per cent cells with free fragments were found in these concentrations. After 24 hours the frequency of free fragments dropped to almost nil. Recovery tests showed that the radiomimetic effects encountered during the treatment were disappearing very rapidly already after few hours.

Remaining secondary effects were rare. The few bridges found may be due to fragmentation in earlier cell generations followed by reunion of chromatids.

Evidently pyrogallol acts on nuclei entering mitosis. Effects on resting nuclei seem to be rare or absent. It was clearly demonstrated that free fragments were induced. Although stickiness was common, the fragmentation was however not of the type of chromatic droplets caused by liquefaction of the chromosomes. A connection between the erosions and the fragmentations seems more likely, extreme points of erosions giving rise to free fragments.

The points of breakage seem to be at random, all sizes of fragments and sometimes as much as 14 fragments in a single cell being found.

Literature cited

- LEVAN, A. and TJÖ, J. H. 1948. Induction of chromosome fragmentation by phenols.—*Hereditas* 34: 453-484.
- LOVELESS, A. and REVELL, S. 1949. New evidence on the mode of action of "mitotic poisons". *Nature* 164: 938.
- THERMAN-SUOMALAINEN, E. 1949. The action of pyrogallol on secondary constrictions.—*Hereditas* 35: 250-251.

Discussion

LOTTI M. STEINITZ-SEARS: Do you have any theory as to how pyrogallol operates in producing the abnormalities? I am asking this, because in experiments on the effects of lack of oxygen on mitosis and meiosis I have found abnormalities very similar to those observed here. In addition, I found that early prophase of both meiosis and mitosis are the most sensitive stages, and that the time taken by the divisions is greatly increased.

G. ÖSTERGREN (Stockholm)

Cytological Standards for the Quantitative Estimation of Spindle Disturbances

In studies on spindle disturbances induced in root tip mitoses by chemical substances it is

often useful to get a quantitative estimate of the degree of influence obtained from the treatment. It might seem easy to make this estimate simply by studying cells with metaphase contraction of the chromosomes and to count the frequency of cells showing a regular arrangement of the chromosomes in a plate. But this method does not work well in practice because there is a stage in the normal chromosome cycle when the chromosomes are irregularly arranged, i.e. the prometaphase stage. For this reason it will be better to consider late stages of mitosis in such a study. The degree of influence is best investigated by counting the frequency of cells with abnormal distribution of the chromosomes (as opposed to the normally bipolar one) during the telophase stage. An example from diethyl bromacetyl carbamide (= adalin) is given.

Reference

The complete version of this paper is published in *Hereditas*, 36, 1950.

Discussion

LOTTI M. STEINITZ-SEARS: Dr. ÖSTERGREN's classification and grading of mitotic abnormalities was most interesting. In our own work we have found it necessary to classify and differentiate sharply between various mitotic abnormalities, and since some of you may be interested in the results I am taking a few minutes to summarize the most significant observations and to give some of the conclusions reached by several members of Dr. C. LEONARD HUSKINS' research group at Wisconsin, with which I was associated from 1946 to 1949.

Briefly summarized the studies of root tip mitoses of several plants treated with sodium ribose nucleate have shown:

1. A temporary upset of cell polarity, so that the spindle direction is at random to the root axis for some time after treatment.
2. A considerable slowing down of prophases and frequently a delayed breakdown of the nuclear membrane. This allows random movement of chromosomes and results in their assuming "grouping" arrangements. In a mathe-

matical paper Dr. KLAUS PATAU has calculated the probable frequencies of various possible "groupings," and our data agree very well with the expectations for his "surface model."

3. When the nuclear membrane breaks down, and frequently even earlier, many nuclei thus show chromosomes arranged into two or more groups. Some of these groupings are maintained throughout meta- and anaphase and give rise to haploid nuclei and occasionally haploid cells, if they happen to contain not only a reduced number but a complete haploid set of chromosomes, e.g. if the separation into groups was also a segregation of homologues.

We have found a high positive correlation between degree of separation of the groupings in meta- and anaphase and the segregation of homologous chromosomes. This correlation is interpreted to show a "force" which keeps apart segregated chromosome sets against the pressure of the spindle. Only such metaphases, with well separated groupings and a high degree of segregation, will give rise to haploid nuclei. Only certain spindle directions in these cells will result in haploid cells. However, these cells, once arisen, may have a fair chance for survival and propagation.

B. KIHLMAN (Uppsala)

Purine Derivatives in the Allium Test

Some twenty purine derivatives have been synthesized, most of which were derived from caffeine by substituting the hydrogen atom at carbon atom 8 with other atoms or atomic groups. The cytological effect of these compounds was tested on root meristems of *Allium Cepa*, according to the usual "onion test" method. The aim of the study was to analyze quantitatively the ability of these compounds to induce structural chromosome changes. Other cytological reactions, such as c-mitosis, c-tumour formation, and stathmodièrèse, also encountered during the investigation, were studied only cursorily and are not reported here.

It was found that most of the purines tested had the same cytological effects as are known from X-ray work, viz., (1) cells undergoing mitosis during treatment showed primary effects (pseudo-chiasmata, stickiness), and (2) cells entering mitosis after a recovery period following the treatment exhibited secondary effects (chromosome breaks and reunions). The efficiency of the various purines tested was, however, highly variable, some being almost inefficient, others having caused structural aberrations in nearly every cell entering mitosis after the recovery period.

The active compounds may be divided into two groups according to their mode of action: (1) ethyl-thio-caffeine and the 8-ethers of caffeine (except 8-methoxy-caffeine) which act rapidly, there being a correlation between dosage and effect, and (2) purines such as caffeine, 8-chloro-caffeine, 1, 3, 7, 9-tetra-methyluric acid, which are effective to a considerable degree only after a long period of treatment, and then only in concentrations sufficiently low to permit mitoses to go on during the treatment. Compounds of both groups probably exert their action during the resting stage; the substances of group (1) seem to penetrate directly into the interphase nuclei through the nuclear membrane, while those of group (2) most likely enter into the nuclei exclusively at telophase. Thus, the difference between the two groups, according to the present hypothesis, is due to a difference in ability of penetration through the nuclear membrane. This implies that the purine derivatives do not act by means of some cytoplasmic derivatives.

Concerning the connection between molecular structure and activity it may be stated that the activity is not bound to any particular atom or groups of atoms but is dependent on the molecule as a whole.

A striking correlation has been demonstrated between the ability of purines to induce structural chromosome disturbances and their solvent power, as it appears from the investigation of WEIL-MALHERBE ("The Solubilization of Polycyclic Aromatic Hydrocarbons by Puri-

nes"—Biochem. Journ. 40, 1946). It therefore seems probable that the solubilizing power, on one side, and the ability to induce structural chromosome changes, on the other, depend on the same properties of the purine molecule.

P. GAVAUDAN et G. BREBION (Poitiers et Le Bouchet par Vert-le-Petit)

L'Echelle des Inhibitions fonctionnelles dans la Cellule végétale

On admet classiquement depuis CLAUDE BERNARD que la cellule végétale soumise à l'influence des anesthésiques est susceptible, comme la cellule nerveuse, d'être le siège d'une narcose. Cette conception a été reprise dans ces dernières années par les chercheurs qui ont étudié le mécanisme d'action des substances cinétoclasiques (1, 2, 3, 4) et l'inhibition de la photosynthèse par les mêmes composés (5, 6, 7).

Nous avons indiqué (5, 6, 7) qu'il existait un certain parallélisme entre les valeurs d'activité thermodynamique, seuil de diverses substances pour l'inhibition de l'assimilation chlorophyllienne, l'action cinétoclasique et la narcose.

Cependant dans ces premières recherches nous avons observé que la colchicine et l'acénaphthène, qui sont des agents cinétoclasiques puissants (provoquant la stathmocinèse), étaient incapables d'inhiber la photosynthèse; ce dernier fait constituait évidemment un obstacle important à la théorie unitaire de la narcose au sens de CLAUDE BERNARD et provoquait une certaine confusion puisque l'inhibition de la photosynthèse paraissait être dissociable de l'action cinétoclasique précédemment assimilée à une forme de la narcose. Soupçonnant qu'une médiocre pénétration de ces substances pouvait constituer un facteur limitant de leur action, nous avons repris nos premiers essais en imprégnant préalablement les tissus sous le vide par les solutions actives (8).

Dans ces conditions assurant une bonne pénétration la colchicine a produit en 8 heures, à la concentration de 1 g/1000, 70 % d'inhibition de la photosynthèse sur *Elodea canadensis* et

50 % sur *Triticum vulgare*, en 8 heures également une solution à 2 g/1000 a produit 100 % d'inhibition (réversible chez *Elodea*); l'acénaphthène à saturation a produit en 8 heures 30 % d'inhibition sur *Elodea canadensis* et 60 à 80 % sur *Triticum vulgare*.

Nous avons aussi étudié l'action des substances cinétoclasiques sur la synthèse de la chlorophylle dans les feuilles de *Triticum vulgare* isolées à partir de germinations étioilées par développement à l'obscurité pendant 10 à 18 jours imprégnées comme il a été dit, puis exposées à un éclairage artificiel continu durant 24 heures. La colchicine à 0,50 g/1000 était inactive; elle inhibait légèrement le verdissement à 1 g/1000 et fortement à 4 g/1000. L'acénaphthène à saturation exerçait une action analogue à la colchicine à 4 g/1000.

En résumé, le benzène exerce une action cinétoclasique à une activité 0,10 et inhibe totalement la photosynthèse et la synthèse de la chlorophylle à l'activité 0,30; l'acénaphthène à l'activité 1 et la colchicine à 4 g/1000 (activité 0,02) qui sont bien entendu cinétoclasiques n'exercent que des actions inhibitrices plus faibles sur la photosynthèse et la synthèse de la chlorophylle. Le benzène s'oppose fortement à la colchicine par la très faible différence entre les valeurs de ses seuils d'action cinétoclasique et des inhibitions portant sur l'appareil chlorophyllien. Cet écart, de 3 à 5 pour le benzène est de 40 environ pour la colchicine en prenant 4 g/1000 pour l'inhibition de la photosynthèse et de la synthèse de la chlorophylle et 0,10 g/1000 pour le seuil d'inhibition de la caryocinèse chez *Triticum*.

Il est bien évident que l'acénaphthène et la colchicine ne sont pas sans action sur la synthèse du pigment assimileur, mais ces substances révèlent l'existence d'un décalage entre les deux types d'inhibitions fonctionnelles qui est d'ailleurs plus accusé chez la colchicine dont le mécanisme d'action est spécial et relève de la classe des toxiques chimiques de FERGUSON (2).

Notons aussi que les deux substances en général les moins toxiques, les moins mitosta-

tiques et n'inhibant jamais la germination sont aussi celles où le décalage est le plus accusé.

Nous concluons qu'au concept d'une narcose unitaire il faut substituer celui plus précis, d'une échelle d'inhibitions fonctionnelles pouvant d'ailleurs être provoquées par des mécanismes différents. Le décalage de l'acénaphthène peut correspondre à un phénomène de « Cut-off » de toxicité (1 et 2), aussi est-il difficile de dire si son existence reflète des degrés différents d'altération d'un même récepteur ou de divers récepteurs. Toutefois le niveau de la marge des activités thermodynamiques dans laquelle sont comprises toutes les inhibitions par les narcotiques indifférents indique une communauté de mécanisme soulignant l'importance de la solubilité et l'analogie avec la narcose typique.

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4. G. ÖSTERGREN, Hereditas 30, 1944, 429-467.
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8. Les utilisations diverses de cette technique seront décrites à part.

SESSION 3

Jointly with Sections EXT, GEN and TPR: July 14th, 2—5 p. m., See page 330

SESSION 4

Jointly with Section MOR: July 17th, 9 a. m. — 1 p. m., Attendance: 70 members

Chairman: F. RESENDE, Recorders: A. LEVAN and F. FAGERLIND

SUBJECT:

Structure and Behaviour of Chromosomes at Mitosis and Meiosis

R. E. CLELAND (Bloomington, Ind.)

Extra Diminutive Chromosomes in Oenothera

Two strains of *Oe. hookeri*, growing 500 miles apart, have shown extra diminutive chromosomes. The first generation of "Mono" showed one plant with 3 extras, and one with two. Ten generations descended from the latter have bred true to the $2n+2$ condition (8 pairs), except for a few $2n+1$ plants. "Mataguey" has been grown through 8 generations from a $2n+2$ plant. It has bred true (8 pairs).

The extra chromosomes in Mono are about half the size of normal chromosomes, in Mata-

guey they are $1/3$ to $1/4$ this size. They pair and disjoin normally in meiosis. Structurally, they resemble the normal chromosomes, with central interstitial region differentiated from the pairing ends. They are not noticeably heteropycnotic. They have shown no tendency to associate with the other chromosomes, their pairing arms not being homologous with any of the 14 ends found in all normal complexes.

Although there has been no tendency toward multiplication of diminutives in selfed line, after the manner of the B chromosomes in maize, outcrosses to other races have frequently produced F_3 s with extra chromosomes. A cross between a $2n$ and a $2n+2$ plant should yield a

hybrid with $2n+1$. Fourteen of the 16 crosses involving Mono have produced F_1 s with $2n+2$ or $2n+3$, the 2 or 3 diminutives being found in all, or part of the buds examined; 7 of the 20 crosses involving Mataguey have shown the same phenomenon. This multiplication might be the result either of non-disjunction, or a more rapid duplication cycle in the diminutives than in normal chromosomes, leading to an occasional double duplication within a mitotic cycle.

Alternate suggestions are offered as to the origin of the extra chromosomes. They may have been derived from another subgenus with smaller chromosomes, such as *Anogra*, by way of an outcross which produced a viable F_1 plant from which a gamete was transmitted possessing a full hookeri complex plus one chromosome from the other race. Or they may have arisen as a result of fragmentation following non-disjunction or polyploidy, producing a centric fragment which through a subsequent fragmentation came to consist only of the central portion of the original chromosome. Differential pairing and chromatid development, such as postulated by WHITAKER (1936), may have permitted formation of new pairing ends.

The extra chromosomes seem to have no phenotypic effect.

Discussion

G. F. L. TISCHLER: Two species, *viz.* *Rhinanthus major* and *Rh. minor*, always seem to have some diminutive extra chromosomes, as FAGERLIND, WULFF and VON WITSCH have found. The original races without these diminutive chromosomes are probably extinct.

G. ÖSTERGREN (Stockholm)

Behaviour of Chromosomes on the Spindle

A study of the events of mitosis should not so much be directed on the purpose of testing the value of a number of more or less preconceived alternatives, such as traction fibres, electrical forces, cytoplasmic currents, etc. It

is most probable that no one of these alternatives has much value in explaining the chromosome movements. Instead we should study mitosis with the idea of finding out the laws or rules of chromosome behaviour, such as these are indicated by the events of mitosis themselves. Such a study demonstrates the existence of a number of laws of behaviour, which we must accept irrespective of whether we can give a mechanical explanation of them or not. It is possible to analyze the mitotic events into a number of empirical factors of chromosome behaviour. The most important one of these factors is an attraction of the kinetochores (or centromeres) to the spindle poles by forces increasing in strength with an increasing distance between the kinetochore and the pole. This factor produces both the movement of the chromosomes to the equator during prometaphase and their movement to the poles during anaphase. This attraction also accounts for the auto-orientation of the chromosomes at mitosis and for their co-orientation at meiosis. A probable solution may even be given of the co-orientation in complex rings such as those of *Oenothera*. The behaviour of the chromosomes demonstrates that the spindle does not contain any rubber-band-like fibrils pulling at the chromosomes. The spindle structure is much more dynamic than is implied by some simple variants of the traction fibre idea. Its structure may be related to that of a tactoid. However, the properties of a relatively simple system such as a tactoid will scarcely give a complete description of the spindle which is a part of the living cytoplasm. It is of no importance to decide whether or not we shall attach the label "tactoid" to the spindle. The important point is to find out what the actual properties of the spindle are.

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 Further contributions by ÖSTERGREN will appear in *Hereditas*.

P. MARTENS (Louvain)

Blocage indéfini de la méiose et formation de pseudospores anucléées et aplasmiques chez une Hydroptéridale

Chez *Marsilea hirsuta* BRAUN, les microsporangies adultes contiennent régulièrement 16 microspores volumineuses et de multiples «spores» beaucoup plus petites. L'étude du développement, entreprise depuis plusieurs années avec la collaboration de nos élèves, R. TOURNAY et M.-J. FELLER, a permis d'établir les faits suivants:

1° — Les 16 microsporocytes amorcent la première division réductionnelle; après quoi la méiose est bloquée en métaphase hétérotypique. Ce blocage persiste indéfiniment, mais l'évolution cellulaire se poursuit malgré l'arrêt des phénomènes nucléaires. Elle comporte successivement:

- a) la formation d'une nouvelle paroi cellulosique;
- b) une lente déshydratation, avec réduction de la masse totale du protoplasme;
- c) une contraction progressive de toute la cellule, entraînant sa déformation au sein de l'aire nucléaire primitive et le plissement de sa paroi;
- d) la différenciation et l'épaississement progressifs de cette paroi, qui acquiert les caractères de l'endospore;
- e) la formation centrifuge, grâce à l'activité du tapis plasmodial, de l'épaisse «couche striée» de l'exospore, sans contact continu et à une certaine distance de l'endospore;
- f) la contraction ultérieure de cette couche, qui tend à rejoindre l'endospore;
- g) la formation des dernières «couches gommeuses» de l'exospore.

Déshydratation, contractions et plissements

sont naturels et non dûs aux traitements. Ils maintiennent, au centre de la cellule plissée, le fuseau hétérotypique étiré, avec ses chromosomes à l'équateur. La figure métaphasique ne se désorganise pas et se retrouve quel que soit l'âge de la spore. Les 16 microspores volumineuses du sporangie mûr sont donc des sporocytes diploïdes en méiose bloquée. Leur comportement chromosomique est à l'étude. Nous n'avons pas réussi à les faire germer.

2° — Les microsporangies contiennent parfois 17 spores au lieu de 16; deux sont alors, contrairement aux autres, non contractées et riches en amidon; ce cas implique l'achèvement exceptionnel de la division I pour un des 16 sporocytes. D'autres sporangies contiennent des spores «multiples», une exospore unique enveloppant plusieurs sporocytes à endospore distincte.

3° — Pendant la différenciation sporale, de nombreuses petites inclusions, généralement lenticulaires, apparaissent dans le protoplasme plasmodial, en périphérie de petite vacuoles. Elles s'enveloppent d'une mince pellicule membranaire, puis d'une couche striée «exosporale», enfin des deux couches gommeuses. Les «petites microspores» du sporangie adulte sont donc des pseudospores anucléées et aplasmiques, mais revêtues cependant d'une paroi «cellulaire» aussi complexe que celle des spores authentiques.

Discussion

P. DANGEARD pose une question au sujet de la repercussion des phénomènes cytologiques signalés, sur le cycle évolutif.

G. F. L. TISCHLER: Nous connaissons quelques exemples des Pteridophytes et Angiospermes (p. ex. des microspores chez *Mirabilis* et *Oenothera*, des macrospores chez *Isoetes*, *Selaginella* et *Marsilea*), dans lesquels le cytoplasme est totalement disparu et la membrane est constituée normalement. Elle ne peut pas être une formation morte, mais dans quelque sens une formation métaplasmiqne nourrie par des cellules voisines du tapis.

A. LIMA-DE-FARIA (Lund)

The Chromosomes of Secale cereale at Pachytene

The seven chromosome pairs of the normal complement of *Secale cereale* (A chromosomes) along with the "standard fragment" (a type of B chromosome) have been identified at pachytene. The size of the chromosomes and of the arms has been determined. It has also been possible to investigate the number, size and sequence of the chromomeres of each chromosome.

Each chromosome pair is recognized by 1) its arm ratio, 2) the characteristic position and size of knob formations (seriations of big chromomeres), 3) particular seriations of big and small chromomeres, and 4) the total chromomere number. The total number of knob formations of the whole normal complement plus the standard fragment pair is 12, of these ten are terminal and two intercalary, one of them forming part of the nucleolar organizing region. The total number of chromomeres of the whole normal complement plus the standard fragment pair is 686 (this value is the mean of a total of 44 analysed chromosome pairs). The analysis of chromosomes I, II and VII gave the mean values of 102, 102 and 100 chromomeres, respectively; of chromosomes III, IV, V and VI the mean values of 89, 87, 84 and 82 chromomeres, respectively; and of the standard fragment 40 chromomeres.

Not all chromomeres are found in pairs; there are chromomeres which have no partner. In other cases the two chromomeres of the same pair are of different size. This evidence of the partial heterozygosity of the chromosome material of rye is in agreement with the cross-fertilizing breeding system of the species.

Cytological maps of the whole complement and of the standard fragment at pachytene are under preparation.

The plants studied originated from a cross between an inbred line and Vasa II rye, the latter parent plant with two standard fragments. The preparations were made by using a modified iron-aceto-carmin technique.

A series of preparations showing the seven chromosome pairs and a pair of standard fragments at pachytene have been exhibited during the Congress.

W. E. DE MOL VAN OUD LOOSDRECHT
(Amsterdam)

The Mercury Lamp in the Service of Microscopic Researches

Especially for microscopic researches that require capital magnifications with oil immersion, a strong source of light is of considerable importance.

As moreover the current of light should under any circumstances be constant and of a similar quality, only artificial sources of light deserve consideration.

The Wolfram arc-lamp, which up till now has been widely used, has two major disadvantages:

- (1) the construction is rather complicated,
- (2) the difficulty remains that with such a lamp the light intensity cannot be much increased.

In the last few years Messrs Philips Ltd. have constructed a new source of light, the light of the so-called super-high-pressure-mercury lamp, which at an extraordinary high effect effuses a potent and strong current of light (by effect, the supplied energy in proportion to the effusion of light energy is understood). I used this lamp with considerable success for my microscopic researches of the cells, the nuclei and the chromosomes of flower bulbs.

I always used the so-called HP 80 W lamp (formerly known as HP 300). The necessity of the use of a pre-switching apparatus, however, and the more complicated construction of this lamp compared with the incandescent lamp, makes its price considerably higher, but the consumption of current is considerably lower. A more intensive source of light is obtained for a certain amount of W. The HP 80 W procures 3000 lumen for 83 watt, while an incandescent

lamp of 3000 lumen requires 205 watt. Moreover the average resistance of the HP lamp is 2000 light-hours, whereas that of the incandescent lamp amounts to 1000 light-hours.

Also, there is a large difference in the colour of the light—the HP lamp shows a much more favourable spectrum of rays.

About the technical features of the microscope lamp I have designed, I want to mention the following data. Nothing of the lamp itself is visible outside, for the lamp is fitted in a special protection bulb opening to the front, reflecting the light on the mirror of the microscope. The protection bulb is revolving on a hinge which can be fastened with an adjusting screw. In this way it is possible to move the light up and down circularly.

Being placed on a stand, this can be brought into a vertical motion with the aid of an adjusting screw. As the protection bulb acquires a high temperature after the lamp having burned a few minutes, the cap is provided with a fibre knob. This makes possible any motion of the lamp in front of the microscope during experimentation.

In order to obtain an equal current of light on the mirror, it proved insufficient to provide the protection bulb with a round diaphragm, but this had to be substituted by a rectangular shell, working as a streak of light. It was also necessary, with regard to the continuous current of light in front of the microscope, not to direct

this to the heart of the lamp but to mount it excentrically.

The spectral division of the light effusion of the HP 80 W lamp proves to contrast favourably with that of the common incandescent lamp, because in the latter the red inconveniently predominates.

The study of microscopic preparations is very exerting, especially with large magnifications. With the aid of the HP lamp, I and many others using it experienced *a more restful image with less exertion*.

It is a well-known fact that for a minute observation it is of no purpose to enlarge more intensely than 1000 \times ; otherwise the picture is growing darker and duller with ensuing difficulties in observation. The theory that minute details could be better observed by stronger magnification is entirely at variance with the sound theory about microscopes. This holds also true for the HP lamp. In magnifications of 1 to 1000, chromosomes are easiest to count and discernable, while those of 1 to 2650 are always practised for the drawing of chromosomes, by means of a drawing-prisma.

A magnification of 1 to 2650 (surface of the picture at the same level as the table on which the microscope is standing) is not the strongest. This may be raised up till 3300 by using an apochromate objective. It was, however, of no use for the study of chromosomes to magnify the reproduction of the outlines in this way.

SESSION 5

Jointly with Section MOR: July 17th, 2—8 p. m., See page 361

SESSION 6

Jointly with Sections GEN and MYC: July 18th, 9 a. m. — noon, See page 424

SESSION 7

Jointly with Sections AGR, EXT and GEN: July 18th, 1—4 p. m., See page 174

SESSIONS 8 AND 9

Jointly with Sections EXT, GEN and TPF: July 19th, 9 a. m.—1 p. m., and 2—5 p. m., See page 277

SESSION 10

Jointly with Sections EXT and GEN: July 20th, 9 a. m.—1 p. m., Attendance: 75 members

Chairmen: R. R. GATES and Ö. WINGE, Recorders: G. ÖSTERGREN, G. TURESSON and Å. GUSTAFSSON

SUBJECT:

Mutation Problems and Structural Chromosome Changes

H. MARQUARDT (Freiburg im Breisgau) *Abbauprodukte körpereigener Stoffe als mutagene Agentien*

Die mutagene Wirkung der verwendeten Agentien wird an den Chromosomen der Meiosis festgestellt, die im Ruhezustand oder in frühen Stadien das Agens verabreicht erhielten. Die Berechtigung, aus dem Auftreten von Rekombinationen zusammen mit Fragmentationen in einer ersten Kernteilung nach der Behandlung (direkte Methode) auf mutagene Wirkung zu schliessen, wird in der Tatsache gesehen, dass alle bisher bekannten mutagenen Agentien sowohl Chromosomen-Mutationen wie auch mit Hilfe der genetischen Methode feststellbare Punktmutationen auslösen. Beide Methoden fassen somit verschiedene Seiten desselben Geschehens.

Samenextrakt von 1- und 10-jährigen *Oenothera*-Samen wurde in Knospen von *Paonia tenuifolia* 4 Tage vor der Metaphase der Meiosis injiziert. Gegenüber einer reinen Wasserinjektion ist bei beiden Extrakten der Prozentsatz der Rekombinationen und Fragmentationen um das 4–5-fache erhöht, so dass dem Samenextrakt beider Altersstufen eine mutagene Wirkung zugesprochen werden muss. Gleichzeitig wird die Chiasmafrequenz um durchschnittlich 1 Chiasma pro Zelle gesenkt. — Abgeschnittene Infloreszenzen von *Oenothera Hookeri* werden in

Samenextrakt derselben Samensorten wie in der ersten Versuchsserie bei 10° Konstanttemperatur gestellt, so dass die Lösung durch den Transpirationsstrom aufsteigt; nach 6 Tagen wurde die Meiosis fixiert. 1- und 10-jähriger Samenextrakt ergibt keinen höheren Prozentsatz von Chromosomen-Mutationen als die Kontrolle, doch beeinträchtigt der ebenfalls vorhandene Bindungsausfall (Senkung der Chiasmafrequenz) die Erkennung von Chromosomen-Translokationen. Entweder wird somit hier der Samenextrakt auf dem Wege zu den reduzierenden Knospen bis zur Unwirksamkeit verändert oder er wirkt nicht mutagen auf *Oenothera*. — In einer dritten Versuchsserie wurden *Oenothera Hookeri*- und *Oe. franciscana* × *Hookeri*-Infloreszenzen (letztere mit 1 Viererring in der Meiosis) in 1,5-prozentige Lösung von Putrescin-Dihydrochlorid bei 10° Konstanttemperatur gestellt und nach 6 Tagen die Meiosis fixiert. Bei *Oenothera Hookeri* trat eine Zunahme der Chromosomen-Mutationen ein, welche die Wirkung von 150 r Röntgenbestrahlung von Freilandpflanzen um fast das doppelte übersteigt; bei dem *Oenothera*-Bastard enthielten 40 % der Zellen Chromosomen-Mutationen. Die starke Reaktion des Bastards auf das mutagene Putrescin entspricht den Befunden von OEHLKERS an *Oe. suaveolens* × *Hookeri* (*flavens Hookeri*) mit Äthylurethan. Putrescin erweist sich somit als stark mutagene Substanz. Ebenso wie bei

Röntgenbestrahlung wird die Zahl der Endbindungen (Chiasmafrequenz) nicht verändert.

Die wirksame Stoffgruppe im *Oenothera*-Samenextrakt muss im Verlaufe normalen Stoffwechsels entstanden sein. Amine, denen das Putrescin zugehört, kommen in der Blüte als Duftstoffe vor, ferner ist in der Wurzel von *Atropa* das Putrescin selbst als Proalkaloid nachgewiesen. Es wird aus den experimentellen Ergebnissen daher der Schluss gezogen, dass auch durch natürliche Stoffwechselprodukte der Zelle auf den Kern mutagene Wirkungen ausgeübt werden können. Eine weitere Bestätigung dieser Auffassung wird in 2 Versuchsserien erbracht: Injektion von aqua destillata in die Knospen von *Paeonia tenuifolia* führt zu einer Zunahme der Fragmentationen, aber nicht der Rekombinationen. Abschneiden der Infloreszenz von *Oenothera* und Aufsteigen von aqua destillata bei 10° Konstanttemperatur führt zu einer Steigerung der Chromosomen-Mutationsrate (vor allem Rekombinationen) auf etwa das 10-fache gegenüber Freilandpflanzen. Die Meiosis ist also ein so empfindlicher Vorgang, dass Störungen der normalen physiologischen Situation ausreichen, um eine Erhöhung der Chromosomen-Mutationsrate zu bewirken. Sie erscheint daher als Test auf mutagene Wirkungen viel empfindlicher gegenüber der Mitose, welche z. B. auf tiefe und hohe Temperatur sowie auf Temperaturschock nicht mit Chromosomen-Mutationen reagiert.

Für die allgemeine Frage der Bruchentstehung auf den Chromosomen wird aus diesen Ergebnissen der Schluss gezogen, dass ausser einer direkten Einwirkung des mutagenen Agens auf die Chromosomen auch eine indirekte Einwirkung über pathologische Stoffwechselprodukte berücksichtigt werden muss. Die bisherigen biophysikalisch orientierten Hypothesen der Bruchentstehung werden daher als nicht mehr ausreichend angesehen. Es wird eine neue Hypothese vorgetragen, welche auch die Möglichkeit indirekter Bruchentstehung zulässt und der grossen Zahl von neueren, schwer mit der treffertheoretischen Interpretation zu vereinenden Befunden gerecht wird. Sie

schliesst gleichzeitig den normalen Vorgang der Chiasmabildung in der Prophase der Meiosis ein.

Discussion

F. RESENDE: In Wurzelmeristemen von *Trilium* fand SALORD (Bol. Soc. Port. Ciênc. Nat.:16) eine starke Fragmentation der Chromosomen zusammen mit dem Primäreffekt nach Einwirkung einer Temperatur von -9°.

E. KNAPP: 1. Nach den zahlreichen vorliegenden Befunden scheint es doch so, dass bei Einwirkung der kurzwelligen energiereichen Strahlung, einschliesslich des U. V., im wesentlichen eine direkte Wirkung auf die genetische Substanz der Chromosomen im Sinne der Treffertheorie vorliegt und offenbar werden auch Chromosomenbrüche so ausgelöst. Die Befunde mehrten sich aber, und der Vortragende hat weiteres schönes Material dafür beigebracht, dass daneben auch vielfach mit indirekten Wirkungen der verschiedensten mutationsauslösenden Agenzien zu rechnen ist. Es wird zu klären sein, ob es sich dabei immer nur um ein auf einer Beeinflussung der physiko-chemischen Eigenschaften der Chromosomensubstanz beruhendes Zerschneiden oder Zerreißen der Chromosomen handelt und ob auch die genetischen Veränderungen auf die so verursachten Brüche und anschliessende Rekombinationen zurückzuführen sind. — 2. Es fällt auf, dass schon bei Verwendung von Extrakten aus 1 Jahr alten Samen eine so starke Erhöhung der Mutationshäufigkeit festgestellt wurde und dass bei Verwendung von Extrakten aus 10 Jahre alten Samen keine weitere Steigerung auftrat. In den Untersuchungen von STUBBE an *Antirrhinum* konnte erst nach mehrjähriger Alterung des Samens eine deutliche Erhöhung der Häufigkeit mendelnder Mutationen nachgewiesen werden. — 3. Nach Einwirkung von Putrescin wurde bei *Oe. franc.* × *Hookeri* eine wesentlich grössere Häufigkeit von Chromosomen-Mutationen als bei *Oe. Hookeri* gezeigt. Es wäre interessant zu wissen, wie sich die spontane Häufigkeit der Mutationen bei *Oe. franc.* × *Hookeri* im Vergleich zu *Oe. Hookeri* verhält.

J. W. and MARGARET M. LESLEY
(Riverside, Calif.)

*A Cytogenetic Study of a Pleiotropic Mutant
of *Lycopersicon esculentum**

A new simple recessive gene mutant of the tomato named "cabbage," with the symbol *cb* occurred spontaneously in our cultures. The number and variety of differences from normal sibs is exceptionally great. Cabbage has darker-green leaves, inconspicuous inflorescences, fewer and smaller fruits, also fewer flowers per inflorescence and fewer loculi per ovary. Unilocular ovaries were more frequent in cabbage. Fertility is greatly reduced. Cabbage has typically the diploid number of chromosomes. Its unfruitfulness appears to be due to general physiological causes rather than to chromosome abnormality. The cells of the sporogenous tissue of the small and often shrunken anthers vary greatly in size. Their size difference is continued throughout meiosis. In the large diploid pollen mother cells of cabbage, the nuclei and nucleoli are larger than in the smaller diploid cells. Apparently the primary cause of increased nucleus and nucleolus size is cell size rather than increase in chromosome number or satellite size. During the last somatic division preceding meiosis there is a strong tendency toward total or partial failure of cytokinesis in the mutant. This may give rise to large pollen mother cells with two diploid prophase nuclei. In such cells reduction proceeds simultaneously in the two nuclei so that eight haploid microspores are usually formed. But three diploid and two haploid nuclei were found in one cell, indicating that restitution nuclei are sometimes formed at second anaphase or after. Tetraploid pollen mother cells occur in the mutant from the fusion of the two prophase nuclei of binucleate cells. In a cell with two diploid nuclei non-reduction may occur in both. In one case non-reduction appears to have occurred in a tetraploid pollen mother cell. Occasional tetraploid or binucleate pollen mother cells have been found in normally fruitful sibs of cabbage.

These are believed to be due to incomplete dominance of the normal allele.

While some single-gene mutants of the tomato have only one known effect, others are pleiotropic, using the term in the etymological sense of "in many ways or modes." The *d*₁ or dwarf mutation affects numerous organs of the plant and was formerly known as a subspecies. The mutant cabbage is even more remarkable for the number and variety of differences from the normal. This diversity of effects suggests that the pleiotropy of cabbage may be "genuine" or "gene-active," using the terms proposed by GRÜNEBERG (1938) and by ADORN (1948). The occurrence of a single gene - single effect relation in *Neurospora* is strong evidence against the existence of gene-active pleiotropy in that organism but perhaps there has been a tendency to select mutants with single effects or to overlook secondary effects. In the case of cabbage and of dwarf, no evidence suggesting that the pleiotropy is due to several closely linked genes has been found. Cabbage appears to be a single gene mutant of somewhat reduced viability. The locus is in chromosome III and 28 crossover units from *y*, the mutant gene for non-yellow skin color of the fruit.

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W. E. DE MOL VAN OUD LOOSDRECHT
(Amsterdam)

*Somatic Mutation in Tulips by Treatment
with Neutrons*

In the year 1943 I treated 500 tulip bulbs with neutrons. The irradiation was effected with the aid of a neutrons generator, in the period from November 3rd till 12th.

As a radiation source the atomic nuclear

reaction of Li with swift neutrons was used. To slow down the speed of the evading swift neutrons the Li-holder had been surrounded from all sides with paraffin.

In this room the bulbs to be irradiated were placed. Between the bulbs and the Li-holder was 1 cm of paraffin and 1 cm of lead. The bottom and both sides were covered with 5 mm of lead. This lead protection served to take away the X-rays from the discharging room of the generator (hardness 50 KV).

The irradiation periods have been taken rather on good luck: $\frac{1}{2}$, 1, $1\frac{1}{2}$, 2 and 4 hours.—Of all the experiments so patiently and accurately arranged only one neutrons-mutation can be considered a success, namely, the variety acquired out of the tulip Utopia.

A flowerbud of Utopia has, shortly before bloom, a length of 51 mm and a breadth of 22 mm; neutrons-mutation 55 and 30 mm. Flower of Utopia: length 74 mm, breadth 71 mm; neutrons-mutation 80 and 89 mm.

Perigon leave of Utopia: length 75 mm, breadth 69 mm; neutrons-mutation: 83 and 72 mm.

As the space in these Proceedings is only limited, I am not now in a position to give further details as to the practical results gained with irradiation—but I will gladly supply these to those who happen to be interested.

The experimental as well as the theoretical atomic physics of the last few years have sufficiently proved that a division in electromagnetic radiations (or wave radiations) and corpuscular radiations may no longer be considered valid as to their acuteness. The electromagnetic radiations much more possess certain qualities which up to the present are only observed with corpuscular radiations which could be explained, at least in these cases, only if a wave-character was attributed to the corpuscular radiation.

Corpuscular radiations mostly consist of small corpuscles which are moved and charged (alpha rays, beta rays, etc.). They, however, may have very different qualities. In our experiments we have only to deal with irradiation

with uncharged corpuscles (neutrons). We know that a neutron has about the same mass as a hydrogen atomic nucleus and that it essentially distinguishes itself from the latter by being uncharged.

It may be supposed as generally known that the biological effect of neutrons-radiation cannot easily be overlooked on account of its complicated absorption mechanism. Does it only make itself known after several ionisation processes? Is the neutrons-radiation as unspecific as that of the remaining corpuscular radiations?

Up till now I have much better results for the acquiring of bud mutations with X-radiation than with neutrons-irradiation.

H. MATSUURA (Sapporo)

On the Structural Aberration of Chromosomes Found in Natural Populations of Trillium

During five years of investigation on *Trillium*, several plants which show various structural aberrations of chromosomes were found in its natural populations. These are classified as follows.

1. Reciprocal-translocated. Here two types are distinguished; one is reciprocal translocation between parts of two particular chromosomes of a complement (its normal members being A, B, C, D, and E) and the other is characterized by reciprocal translocation between the entire arms of two particular chromosomes. The former will be designated as "partial translocation" and the latter as "entire translocation." Up to the present, two plants of *T. kamschaticum* were identified to be of the latter type, one being the translocation heterozygote between the short arm of D and the short arm of E, and the other between the short arm of B and the long arm of E.

2. "Dislocated." Here the term "dislocation" means that a single chromosome is divided into its two arms which function normally, although it does not necessarily imply that such two chromosomes were originated simply by

the misdivision of the kinetochore. Such a unique plant was found in a population of *T. Hague* (triploid). The chromosome involved here is A, the two other homologues being normal.

3. Di-kinetic. Some plants of *T. kamschaticum* were shown to be di-kinetic. The chromosome involved here was in these plants always B, its one member having two kinetochores lying side-by-side and the homologue being normally mono-kinetic.

These aberrant plants are those found among several hundreds of individuals growing under natural conditions. "Partial translocation" has not been found independently; it was identified only in "dislocated" and di-kinetic plants.

These plants show interesting features of meiotic chromosome behavior. The essential points quite agree with the writer's neo-two plane theory regarding bivalent formation and the disjunction of the paired kinetochores. As to the origin of these plants under natural conditions, a possible mechanism is indicated by the writer's data from another aberrant plant of *T. kamschaticum*, "sticky", in which all chromosomes tend to stick together in the PMC's and various chromosome aberrations are induced at the first meiotic metaphase. Its mechanism quite agrees also with the writer's spiral theory of crossing-over.

SOPHIA SATINA and A. F. BLAKESLEE
(Northampton, Mass.)

Chromosomal End Arrangements due to Segmental Interchange in Ten Species of Datura

Segmental interchange discovered by BELLING had been found by BERGNER to occur in evolution of *Datura* species. All *Daturas* have 12 chromosomal pairs with 24 kinds of ends. Tests of chromosome attachments at MI in hybrids between a standard American line and over 700 races in nature disclosed 5 recurrent and 5 sporadic chromosomal types (Prime Types) in *D. stramonium* with interchanged chromosomes in terms of the standard Prime

Type 1. Pairing indicates homologous ends; configurations of 4 or more chromosomes indicate rearrangements of chromosome ends. Radiation and aging of seeds induced segmental interchange from which 86 additional homozygous Prime Types have been secured in *D. stramonium* and used in identification of chromosome ends in hybrids with other species.

Prime Types have been found in all *Datura* species in which an adequate number of races has been tested. Difficulties in securing species hybrids have been only partially relieved by "bridging species" and embryo culture. However, end arrangements have been determined in all 10 species except *D. meteloides* in which half the chromosomes are determined.

Our standard Prime Type 1 *D. stramonium* is not the most common chromosomal form and probably not the most primitive. A Prime Type of one species may have the same end arrangements as those of another species and races of two species may have only two chromosomes with the same end arrangements. There is no direct correlation evident between segmental interchange and either taxonomic differences or crossability but segmental interchanges may serve as cryptic characters with which to trace evolutionary relationships. Certain chromosomes are relatively stable. Thus the 5.6 chromosome has suffered an interchange only in *D. innoxia* and *D. meteloides*; in contrast the 11 half chromosome has taken part in 7 different kinds of interchanges. By combining the proper Prime Types, pure breeding forms have been secured with terminal extra chromosomal material. Separate interchanges between two chromosomes may be at different levels. By crossing such types, plants homozygous for the larger interchanged chromosomes have been secured which are pure breeding types with an excess of certain internal chromosomal material.

Discussion

P. N. BHADURI: I would like to point out that we have found a very interesting situation in the case of *Datura metel* (white flowered

variety) which grows wild round about Calcutta. This observation has shown that pollen mother cells in the same anther locus may have different chromosome numbers, a fact which I have explained on the basis of premeiotic irregularities (BHADURI, P. N. and SHARMA, A. K.—Bull. Torr. Bot. Club 1947). This indicates that there might be *D. metel* in nature with $2n = 24$ chromosomes but showing chains of three or quadrivalents without involving segmental interchange.

E. KNAPP: Es wäre interessant zu wissen, wo die Brüche liegen und wie gross die ausgetauschten Chromosomenstücke sind, die zu den verschiedenen Chromosomen-Enden der verschiedenen Primärtypen führen.

H. MARQUARDT: In your table, you demonstrated that in certain plants there occurred configurations of \odot and of \odot . Is it possible that these have arisen by chiasmata in the interstitial segment (the segment between the centromere and the translocation point)?

R. BAUCH (Greifswald)

Mutationsauslösung durch Trypaflavin

Der Akridinfarbstoff *Trypaflavin*, dessen Mitosegiftwirkung von DUSTIN erkannt war, löst an der pflanzlichen Wurzel (*Allium*-Test) die gleichen zytologischen Erscheinungen aus wie die Bestrahlung mit Röntgen- oder Radiumstrahlen. Verklebungen der Tochterchromosomen während der frühen Anaphasen, die auf kolloidchemischer Veränderung der Chromosomensubstanz beruhen, führen zu der Gesamtheit des *Pseudoamitosen*-Komplexes, wie er bereits 1934 von POLITZER geschildert worden war. Hinzu kommen Fragmentationen der Chromosomen, die häufig zur Bildung von Kleinkernen führen und die unter Umständen das Chromosomengefüge völlig zersprengen. Der *Trypaflavin-Effekt* wird schon durch einstündige Behandlung mit stark verdünnten, eben noch sichtbar gefärbten Lösungen (10^{-6}) ausgelöst. Dabei wirkt die Substanz nicht nur auf die gerade im Ablauf befindlichen Mitosen, sondern

gleichsinnig auch auf die Ruhekerne. Kultiviert man die Wurzeln nach kurzzeitiger Behandlung in Wasser bis zur Bildung von Seitenwurzeln (ca. 20 Tage) weiter, so treten auch in den Seitenwurzulanlagen die Gesamterscheinungen der Pseudoamitose auf. Da diese Seitenwurzeln auf Zellen des Perizykels zurückgehen, die sich zur Zeit der Behandlung sicher im inaktiven Zustand des Ruhestadiums befanden, ergibt sich aus diesen „Erholungsversuchen“ die Tatsache, dass der Farbstoff auch auf die entspiralisierten Chromosomen der Ruhekerne einwirkt und dass der einmal gesetzte Effekt zu einer irreversiblen Schädigung der chromosomalen Substanz führt. Wie weit nach der Trypaflavin-Behandlung auch Restitutionen der abgesprengten Chromosomenfragmente vorkommen, unterliegt noch genauerer Prüfung.

Die Fluoreszenz des Trypaflavins erlaubt nun eine weitergehende Analyse seiner radiomimetischen Wirkung. Ruhekerne speichern den Farbstoff selbst aus höchst verdünnten Lösungen (2×10^{-7}) innerhalb kurzer Zeit (*Allium*-Epidermis), während das Plasma ungefärbt bleibt. Bei den Prochromosomenkernen der Cruceiferen speichern ihn innerhalb des Kernes nur die Prochromosomen selbst. Er wird also selektiv von der chromosomalen Substanz selbst gebunden. Die Riesenkerne der Speicheldrüsen von *Chironomus* und *Drosophila* geben eine spezifische Speicherung in den Bändern, während die Zwischenscheiben ungefärbt bleiben. Da die Bänder der Riesenchromosomen nach CASPERSSON besonders reich an Nukleoproteiden sind und da sich andererseits im Reagenzglas die Bildung von salzartigen Verbindungen zwischen Trypaflavin und Nukleinsäure nachweisen liess, dürfte aus diesen Befunden der Schluss zu ziehen sein, dass auch *in vivo* spezifische chemische Veränderungen an den Nukleoproteiden der Kerne bzw. der Chromosomen durch Trypaflavin ausgelöst werden. Da andere Akridinfarbstoffe mit besonderer chemotherapeutischer Wirksamkeit wie *Atebrin* und *Rivanol* die gleichen zytologischen Effekte verursachen wie Trypaflavin, dürfte die Malaria-Wirkung dieser Substanzen ebenfalls auf eine

radiomimetische Schädigung der Parasitenkerne durch Nukleinatbildung zurückzuführen sein.

Angeichts der weitgehenden zytologischen Ähnlichkeit zwischen Bestrahlungsreiz und Trypaflavineffekt wurde die Frage geprüft, ob durch Trypaflavin im gleichen Sinne wie durch Bestrahlung Mutationen ausgelöst werden. Durch H. J. OVERBECK wurde diese Frage in einer Dissertationsarbeit an *Lepidium* und *Stenophragma* überprüft. *Stenophragma* eignete sich für diese Untersuchungen ganz besonders, da die Mutabilität dieser Crucifere vor kurzem durch REINHOLZ (1945) im Röntgenversuch überprüft worden ist. In der F₁-Generation nach Samenbehandlung traten tatsächlich verschiedenartig veränderte Formen auf, die in der F₂ zahlreiche weitere Veränderungen herauspalten liessen. Da der Mutationscharakter dieser neuen Formen z. Zt. noch überprüft wird, bezeichnen wir sie vorerst als Variationen. Bei *Lepidium* wurde der Prozentsatz der Variationen von 2,5 % der Kontrolle auf 15,1 % durch Trypaflavin-Behandlung erhöht. Bei *Stenophragma* erweiterte sich die Variabilität von 0,6 % auf 7,7 %. Bei dieser Pflanze entsprachen die neuen Formen mehrfach den durch REINHOLZ erhaltenen Röntgenmutanten. Die Variationsprozente können also wirkungsmässig einer schwachen Röntgendosis von ca. 1000–1500 r gleichgesetzt werden. Ebenso wie nach Röntgenbestrahlung werden auch nach Trypaflavinbehandlung der Samen Stimulationerscheinungen beobachtet.

Es dürfte daher zu erwarten sein, dass durch weitere Untersuchungen mit anderen radiomimetisch wirksamen Substanzen (Glykol, Kumarin, usw.) tiefere Einblicke in den Ablauf der Strahlenwirkung zu erhalten sein werden.

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Discussion

C. HARTE: Ist die Nachwirkung des Trypaflavins über mehrere Wochen nur durch eine Beeinflussung der Ruhekerne zu erklären oder auch durch eine Nachwirkung des in der Pflanze gespeicherten Trypaflavins?

R. BAUCH: Es ist mit Sicherheit anzunehmen, dass hier eine Beeinflussung der Ruhekerne vorliegt und nicht eine Nachwirkung des gespeicherten Trypaflavins. Die Behandlung mit Trypaflavin braucht zur Auslösung des zytologischen Effektes nur kurzfristig (1 Stunde) zu sein. Das Wurzelmeristem wächst aus der gefärbten Zone heraus und ist nach 1–2 Tagen weiteren Wachstums schon völlig farblos. Seitenwurzeln, die nach 2–3 Wochen entstehen, sind völlig ungefärbt, sie zeigen aber die charakteristischen radiomimetischen Kerneffekte.

H. KUCKUCK: Ist etwas näheres über den Stimulationseffekt bekannt? Kann hier die Heterosiswirkung von subletalen Genen im heterozygotischen Zustand vorliegen, die durch Trypaflavin ausgelöst sind?

R. BAUCH: Der Stimulationseffekt ist noch nicht genauer analysiert worden.

E. KNAPP: 1. Handelt es sich bei der Auslösung von Mutationen durch das fluoreszierende Trypaflavin ausschliesslich um eine rein chemische und nicht um eine photodynamische Wirkung wie bei der Wirkung des Eosins in den Untersuchungen von DÖRING an *Neurospora*?

2. Wenn sich tatsächlich nachweisen lässt, dass das Trypaflavin vor allem durch die Nukleinsäure absorbiert wird und wenn diese Absorption des Trypaflavins durch die Thymonukleinsäure für die Mutationsauslösung verantwortlich ist, so wäre das auch insofern von Bedeutung, als sich nach Untersuchungen an *Sphaerocarpus* (KNAPP 1939) gezeigt hat, dass die Häufigkeit der durch die verschiedenen Wellenlängen des U. V. ausgelösten Mutationen parallel geht der Absorptionskurve des U. V.

durch die Thymonukleinsäure, dass also die von der Thymonukleinsäure absorbierte Energie verantwortlich ist für die Auslösung von Mutationen.

3. Wie sind die „Varianten in F_1 und F_2 “ aufgetreten und ausgewertet worden? Wenn es sich um Punktmutationen handelt, die durch die Behandlung von Samen aufgetreten sind, so wäre, wenn man die Entstehung genetischer Chimären einmal ausser Betracht lässt, zu erwarten, dass Familien aus der Selbstung von Pflanzen, die als Samen behandelt wurden, für die Mutanten spalten, dass also bei rezessiven Mutationen 25 % Mutanten auftreten.

R. BAUCH: 1. Der Trypaflavineffekt an den Kernen tritt auch im Dunklen auf. Es kann sich deshalb nicht um eine photodynamische Wirkung handeln.

2. Trypaflavin bildet mit Hefenukleinsäure

Salze. Seine zytologische und bakterio-statische Wirkung kann durch extrazellulär gegebene Nukleinsäure aufgehoben werden. Trypaflavin wird durch die Scheiben der Riesenchromosomen spezifisch gespeichert. Diese Befunde sprechen dafür, dass seine Wirkung auf einer Reaktion mit den Nukleoproteiden des Kernes beruht.

3. Die mit Trypaflavin behandelte p-Generation zeigt keine Besonderheiten. In der F_1 treten abweichende Formen auf, deren Nachkommen in der F_2 geprüft wurden. In der F_2 -Nachkommenschaft werden verschiedentlich 25 % Varianten beobachtet; in anderen Fällen liegen geringere Prozentsätze vor. Wir führen diese abweichenden Zahlen vorerst auf eine geringere Vitalität der veränderten Keimpflanzen zurück und sind im Augenblick dabei, weitere Generationen zu überprüfen.

EXPERIMENTAL ECOLOGY, EXE

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SESSION 1

July 12th, 2—5 p. m.

Chairmen: W. H. PEARSALL and D. MÜLLER, *Recorder:* L.-G. ROMELL

SUBJECT:

The Ecology of Photosynthesis

DETLEF MÜLLER (Köbenhavn)

Photosynthesis under Field Conditions

No abstract has been received of this paper.

Discussion

B. HUBER referred, for comparison, to experiments made in Tharandt, Germany.

The speaker answered questions on technical points asked by M. G. STÅLFELT, G. E. BLACKMAN, and T. A. OXLEY.

G. E. BLACKMAN (Oxford)

The Integrated Effects of Light Intensity on Net Assimilation Rate, Leaf Area and the Growth Rate of Different Species

Relative growth rate (increase in total plant weight/unit time) is the product of net assimilation rate (increase in total plant weight/total leaf area/time) and leaf area ratio (total leaf area/total plant weight). It therefore follows that if the effects of shading on both net as-

similation rate and leaf area ratio can be expressed mathematically, then the effects of reduced light intensity on relative growth rate can be obtained from the product of the two mathematical expressions.

In an analysis of the effects of shading on the vegetative growth of ten species, plants grown in either pots or in plots have been subjected to light intensities ranging from full daylight to 0.1 daylight. For *all* species it has been established that both the changes in net assimilation rate and leaf area ratio are linearly related to the logarithm of the light intensity. In consequence, the relationship between the logarithm of light intensity (x) and relative growth rate (y) should be curvilinear, i.e. $y = ax^2 + bx + c$, and there is close agreement between the observed and calculated values.

For species of shady habitats (*Scilla non-scripta*, *Gerum urbanum*, *Solanum dulcamara*) neither the net assimilation rate values at different intensities nor the "compensation points"—circa 0.07–0.09 daylight—are very different from those of 'sun' plants (e.g. *Helianthus an-*

nuus, *Fagopyrum esculentum*, *Trifolium subterraneum*). Nevertheless the intensity at which the growth rate is maximal varies between species, e.g. it is full daylight for *F. esculentum*, 0.7 for *H. annuus*, 0.5 for *S. dulcamara*, while with *T. subterraneum* a theoretical value of 1.6 is obtained, demonstrating that for this species full daylight must have limited growth.

These specific differences in the effects of shading on the growth rate are more dependent on the changes in leaf area ratio than on the changes or magnitude of the net assimilation rates. In view of this new analysis of the light factor, a shade plant is best redefined as a species in which the low leaf area ratio in full daylight rises sharply as the light intensity is reduced; for a 'sun' plant, the converse definition holds.

Discussion

Minor questions on points of technique were asked by C. S. FRENCH, E. C. WASSINK, D. MÜLLER and V. J. CHAPMAN and were answered by the speaker.

BRUNO HUBER (München)

Versuche zur Messung des Gaswechsels von Pflanzenbeständen

Der älteren systematischen Botanik folgend, bei welcher heute die pflanzensoziologische Betrachtungsweise im Vordergrund steht, schreitet auch die jüngere Pflanzenphysiologie von der Laboratoriumsforschung über die experimentelle Autökologie zur *Synökologie* fort und be-

müht sich neuerdings besonders um die Messung des Gaswechsels von Pflanzenbeständen.

Die Evaporation-Transpiration lässt sich u. a. nach dem *Wärmehaushaltverfahren* von ALBRECHT als Bilanzrest bestimmen, wenn die übigen Strahlungsumsätze einschliesslich Wärmeableitung nach Boden und Luft genügend genau erfasst werden können. ALBRECHT und BERGER-LANDEFELD haben damit sehr befriedigende Ergebnisse erzielt und beispielsweise den mittäglichen Transpirationsrückgang klar fassen können.

Umfassender ist das *Austauschverfahren* von W. SCHMIDT, welches grundsätzlich jeden Gaswechsel über Pflanzenbeständen als Produkt von Gefällen des betreffenden Gases und Austausch zu bestimmen gestattet. Der *Wasserdampfstrom* wird auf diesem Wege von THORNTWHAITE und Mitarbeitern auf amerikanischen Farmen bereits laufend registriert. Die Badische Anilin- und Sodafabrik Ludwigshafen hat neuerdings im "Thermoflux" ein besonders geeignetes Gerät für die Registrierung der absoluten Feuchtigkeit entwickelt.

Die Registrierung des fünfhundertmal schwächeren CO_2 -Stromes ist dem Vortragenden mit Hilfe des Ultrarot-Absorptionsschreibers derselben Firma gelungen, obwohl die Gefälle nur wenige Tausendstel bis Zehntausendstel Prozent CO_2 betragen. Auf diese Weise lässt sich die Trockensubstanz-Produktion eines Pflanzenbestandes laufend ohne Eingriff verfolgen.

Discussion

M. G. STÄLFELT and Mrs. C. A. REINDERS-GOUWENTAK had minor questions answered by the speaker.

SESSION 2

July 14th, 9 a. m. — noon

Chairman: H. WALTER, Recorder: M. G. STÄLFELT

SUBJECT:

Water Balance

A. PISEK (Innsbruck)

Transpiration und Wasserhaushalt der Fichte bei zunehmender Luft- und Bodentrockenheit

Im trocknen Sommer 1947 und in den nachfolgenden Normaljahren wurden an einem auf sonnigem Hang in Moränenboden freistehenden Baum von 13 m Höhe die Tagesgänge der Transpiration in verschiedener Stammhöhe sonn- und schattenseitig zusammen mit der Evaporation systematisch untersucht (Schnellwägemethode).

Im Vorfrühling steigt die Wasserabgabe sowohl absolut als besonders im Verhältnis zur Evaporation („Transpirationsvermögen“) sprunghaft an, im Spätherbst fällt sie als Zeichen des Überganges zur Winterruhe ebenso steil zurück. In normalen Jahren ohne länger dauernde Trockenperiode transpiriert der Baum im milden Frühlings- und Herbstklima, wenn man die Evaporationsunterschiede zwischen der Licht- und der Schattenseite berücksichtigt, auch an sonnigen Tagen rundherum annähernd gleich und maximal. Im Sommer ist dies nur bei bewölktem Himmel der Fall; an klaren Sommertagen wird dagegen das Transpirationsvermögen der beschatteten Seite, wenn das Sättigungsdefizit der Luft etwa 10 mm überschreitet, zu Gunsten der belichteten Teile eingeschränkt, indem die Schattenzweige auf Unterbilanz ceteris paribus empfindlicher mit Schliessbewegung der Stomata reagieren als Sonnenzweige.

Solange der Wurzelhorizont durchfeuchtet bleibt, ist die Transpiration je Frischgewichtseinheit — absolut und relativ zur Evaporation — an der Kronenbasis in jeder Exposition

grösser als im Wipfelbereich. Wenn der Boden auszutrocknen beginnt, verstärkt der Baum nicht nur die Einschränkung der Wasserabgabe auf seiner Schattenseite, sondern fängt auch bei den besonnenen Zweigen an zu bremsen. Er tut dies aber im untern Kronenteil ringsherum energischer als oben, so dass der Unterschied im Wasserverbrauch und Transpirationsvermögen von Basis und Spitze verschwindet und bei zunehmender Bodentrockenheit sich völlig umkehrt: nun behauptet die Wipfelregion im allgemeinen Rückgang grösseres Transpirationsvermögen als die untern Kronenteile.

Der Baum reagiert als Ganzes auf drohendes Defizit gleich von Anfang empfindlich und es gelingt ihm durch vorsichtige, stufenweise Sparmassnahmen, die besonders die weniger produktiven Teile betreffen, bei zunehmendem Wassermangel die Abgabe weitgehend der Aufnahme anzupassen. Kontrollen des Wassergehaltes und osmotischen Wertes ergaben, dass diese Bilanzzeiger selbst im ungewöhnlichen Trockensommer 1947 in allen Kronenteilen erstaunlich stabil blieben. Solch vorsichtiges und wohlgeordnetes Verhalten dürfte auch für andere Schattenhölzer wie die Buche, in weiteren Grenzen wahrscheinlich für den Baum im allgemeinen (im Gegensatz zu krautigen Pflanzen) typisch sein.

Discussion

B. HUBER: Mittagsdepression zeigt auch die Rinden-Transpiration, weshalb neben der stomatären Regulation auch „incipient drying“ und Abnahme des Interzellularvolumens (NIJS) in Betracht zu ziehen sind.

R. HARDER: Eine endogene Rhythmik im Sinne BÜNNINGS könnte vielleicht eine Rolle

spielen für den Verlauf der Transpiration innerhalb 24 Stunden bei gemässigten Transpirationsbedingungen.

H. R. OPPENHEIMER: It seems surprising that the restriction sets in at first in the shade, though the water balance should be more even there. It would be interesting to know, *where* in the shade the shade figures have been established (whether facing the North, East, or West).

O. STOCKER: Es ist wahrscheinlich möglich, das verschiedene Verhalten der Sonnen- und Schattennadeln auf den protoplasmatischen Faktor zurückzuführen, wobei die ersten sich in der „Abhärtungs-“, die letzteren in der „Verweichlichungsphase“ befinden würden.

This was in reply to a question asked by M. STEINER (Bonn).

R. DARNLEY GIBBS (Montreal)

Seasonal Changes in Water-Contents of Trees

This report deals mostly with trees native to eastern Canada and summarizes work extending over twenty years.

Wood

Betula populifolia, the most-studied species, shows the "expected" pattern with a maximum water-content just before leaf-opening, a minimum at leaf-fall, a partial refilling in the early winter, and a secondary minimum just before thawing of the soil. Other species of *Betula* appear to behave similarly. There is considerable variation from year to year in the case of *B. populifolia*, but the major features of its pattern are retained.

Populus spp. show a somewhat similar pattern but the wood may refill completely in the autumn.

Ulmus americana and *Frazinus americana* have a maximum water-content at leaf-opening and a low value at leaf-fall. They show no autumnal increase, however, and no late winter decrease, remaining "dry" throughout the winter.

Fagus grandifolia has, among the trees investigated, a unique pattern. Its water-content is high in winter, low in the summer. There is no increase in spring.

Several members of the Juglandaceae have been studied to see how closely seasonal changes in water-content are correlated with relationship. Twigs only have been used from these trees. *Juglans nigra*, *J. sieboldiana*, *J. cinerea*, and *J. dracanis* have much the same water-pattern. The two species of *Carya* studied (*C. ovata* and *C. cordiformis*) differ somewhat from *Juglans* but resemble each other. *Pterocarya*, which is taxonomically nearer *Juglans* than *Carya*, resembles *Juglans* rather than *Carya* in its water-content.

Comparatively few conifers have been studied in detail. *Tsuga canadensis* is extremely variable and only tentative conclusions may be drawn although 127 trees have been analysed. It had a high water-content in mid-winter, a low water-content in May, a maximum in June, and a secondary minimum at the end of the summer. The seasonal variation is confined to the sapwood.

Pinus banksiana, *Picea canadensis*, and *Abies balsamea* seem to show little seasonal variation in water-content. The heartwoods of the first two are dry: that of the last has curious wet patches that seem not to be connected with the sapwood.

Twigs of *Pinus strobus* and of *Larix europaea* have interesting patterns.

Bark (all tissue external to the wood)

There is much greater uniformity of behaviour in barks than in woods.

Practical Importance of the Results

Brief reference is made to the problems of flotation and to possible weight-saving in the transportation of logs by land.

Discussion

B. HUBER: Die Wassergehalts-Schwankungen des Holzes verschiedener Bäume stimmen ziemlich mit den Besonderheiten ihres Tran-

spirationsstromes überein. *Nadelhölzer*: gleichmässig hoher Wassergehalt im Splint, trockener Kern. *Zerstreutporige Laubhölzer*: Sättigung des Splints im Frühjahr, Defizit im Sommer, Erholung im Herbst, langsame Abnahme im Winter, Kern gleichmässig trocken (*Fagus*). *Ringporige Laubhölzer*: Schwankungen nur im jüngsten Jahrring, sonst Trockenkern.

Vorläufig unverständliche Ausnahme: *Tannen-Nasskern* (*Abies*); bedarf weiterer Untersuchung.

E. W. J. PHILLIPS had questions about the absorption of water by floated logs and about wet patches found in lumber from Western Canada.

A. R. A. TAYLOR: Has any morphological difference been observed between the "wet" and "dry" patches of *Abies balsamea*?

R. D. GIBBS: No anatomical observations have been made.

CHARLES KILLIAN (Alger)

Le bilan hydrique et l'échauffement de végétaux types du Fouta Djallon (Guinée) en saison sèche

Cette étude, basée sur des pesées, après une exposition de 3 minutes, de feuilles coupées, prouve l'intérêt de superposer les courbes journalières transpiratoires à celles des déficits.

Niveaux bas et rapprochés de ces courbes chez les buissons sclérophylles à enracinement profond dans le gravillon latéritique (*Syzygium guineense*, *Mimocylon fasciculatum*, *Haronga paniculata*). Chez les espèces annuelles, rares en saison sèche où les racines en surface ont pu s'abriter sous la rocaïlle, (*Lactuca taraxacifolia*, *Euphorbia pilulifera*), ces courbes sont, au contraire, très distantes l'une de l'autre. Chez les espèces sous-frutescentes de l'argile des bas fonds (*Borreria verticillata*, *Mitracarpum verticillatum*) elles sont distantes le soir et parfaitement énantiomorphes, leur transpiration étant périodiquement freinée par l'exocde du déficit. Enfin chez un xérophYTE *Polycarpaea corymbosa*, humophyte par ses organes souterrains abrités

par les dalles latéritiques, xérophYTE par ses organes aériens, ces déficits atteignent ceux des végétaux sahariens et entraînent un freinage très efficace de sa transpiration.

Entre ce type et ses antagonistes, les sciaphytes de la galerie forestière, se place une liane, *Salacia guianensis*, formant des draperies sur les lisières forestières: elle a les caractéristiques essentielles des buissons sclérophylles mais s'en distingue par la baisse considérable de sa transpiration le matin tôt, due à la fraîcheur nocturne du biotope forestier voisin.

Dans la galerie même, hermétiquement close et très isolée de la savane chaude, règnent des conditions extrêmement équilibrées. Elles permettent la subsistance, en plein été, à des annuelles tendres et aussi à des fougères renaissantes, enroulées en été mais dépourvues de structures protectrices. Pareillement à celles du dehors, à faces inférieures puissamment protégées, leurs courbes sont des paraboles régulières. L'un de ces sciaphytes *Puelia acuminata*, avec un important développement de surface (1,6) est caractérisé, outre par ses courbes plates, par ses puissantes réactions aux fluctuations thermiques momentanées. Il s'oppose par son fort échauffement passager, diamétralement, aux buissons sclérophylles du dehors dont les températures foliaires oscillent autour des températures aériennes, sans régularité apparente. Les écarts maxima entre ces courbes foliaires et les courbes aériennes s'observent, bien entendu, chez notre xérophYTE type.

Si le bilan hydrique et l'échauffement sont dominés par les facteurs microclimatiques, ils dépendent autant des facteurs édaphiques, spécifiques pour chaque biotope.

Les argiles des dépressions, en dehors de la forêt, sont caractérisées par leur tassement estival et leur bonne aération, malgré l'oxydation complète de l'humus. Quant à la terre humifère des galeries elle est de constitution variable, suivant son degré de protection contre la sécheresse de la savane ambiante. Il y a aussi excédant de matières organiques solubles à l'eau, sur la lisière où l'excédant de chaleur

réflexie entrave son utilisation par les micro-organismes.

Discussion

Questions on technical points were asked by R. HARDER and H. VAN VLOTEN.

ALFRED HEILBRONN (Istanbul)

Über die ökologische Bedeutung der ätherischen Öle

Die Tatsache, dass ätherische Öle der Luft beigemischt in wassererfüllten Kapillaren eine Depression erzeugen, beweist, dass diese dem Gibbs'schen Theorem entsprechend von freien Wasseroberflächen absorbiert werden. Wenn also in einem lebenden Blatt wassererfüllte Kapillaren vorhanden sind, ist zu erwarten, dass dieses Wasser, soweit es im flüssigen Zustande ist, in den Kapillaren zurückgedrängt werde. Eine Verringerung des in Dampfform abgegebenen Wassers müsste die notwendige Folge dieser Zurückdrängung sein. An einem leblosen Filtrierpapier-Modell konnte der Verfasser zeigen, dass geringe Mengen verschiedener ätherischer Öle, der Luft beigemischt, in der Tat eine schon nach wenigen Minuten einsetzende Verringerung der Wasserabgabe bewirkten; nach Ersatz der Ölatmosphäre durch frische Luft stieg die Evaporation wieder auf das ursprüngliche Mass. An lebenden Blättern von *Peperomia Sandersii*, die selbst keinerlei ätherische Öle ausscheiden und vollständig geruchlos sind, wurden entsprechende Versuche mit dem Er-

gebnis durchgeführt, dass auch hier, in einer mit ätherischen Ölen versetzten Atmosphäre, die Transpiration herabgesetzt war. Der Versuch, den auf Grund dieser physiologischen Ergebnisse zu fordernden Adsorptionsfilm auf der Blattoberfläche mit chemischen, färberischen oder mikroskopischen Methoden nachzuweisen, musste bei seiner ultramikroskopischen Dicke erfolglos bleiben. Eine elektrische Methode, die darin bestand, das zur Durchschlagung der ein Dielektricum darstellenden Kutikula notwendige Potential zu bestimmen, führte schliesslich zum Ziel. In einer ätherischen Öle enthaltenden Atmosphäre steigt die Dielektrizitätskonstante der Kutikula messbar, wodurch die Aufgabe des Nachweises eines theoretisch zu fordernden Adsorptionsfilms praktisch gelöst sein dürfte. Die ökologische Bedeutung der von Blättern ausgeschiedenen ätherischen Öle liegt also nicht in einem Strahlungsschutz, sondern in einer Herabsetzung der Wasserpermeabilität der Grenzschicht Luft/wasserimbibierte Membran.

Discussion

B. HUBER: Der Erfolg HEILBRONNS kann auf seine elegante Differenzmethode zurückgeführt werden. Absolute Angaben über die Grösse des Effekts wären erwünscht.

A. HEILBRONN: Solche Werte sollen erst bestimmt werden.

M. STEINER: Die Verschiedenheit der ätherischen Öle könnte für die Wirkung von Bedeutung sein.

K. PAECH asked a technical question.

SESSION 3¹

July 14th, 2—5 p. m.

Chairman: B. HUBER, Recorder: M. G. STÄLFELT

SUBJECT:

Drought Resistance

O. STOCKER (Darmstadt)

Begriff und Wesen der Dürre-resistenz

Die ökologische Analyse des Wasserhaushaltes erfordert die gleichzeitige Standorts-

untersuchung der übrigen, von ihm abhängigen physiologischen Funktionen, für welche geeignete Methoden zur Verfügung stehen. Das

¹ This session, like all the following ones, was held in the lecture room of the Eastman Dental Institute.

Ziel ist die Aufklärung der Gesamtkonstitution einer Art und ihrer Abhängigkeit von den ökologischen Umweltbedingungen. Man kann stabile und labile Typen unterscheiden; die ersteren halten auch unter Dürreeinfluss die Funktion wenig verändert aufrecht, die letzteren zeigen grosse Schwankungen. Das Verhalten kann jedoch hinsichtlich der einzelnen Funktionen verschieden sein, wie bei der Zuckerrübe, welche einen sehr labilen Wasserhaushalt, aber eine weitgehend stabile Photosynthese aufweist. In der ökologischen Gesamtleistung brauchen labile Typen nicht minderwertig gegenüber stabilen zu sein, da sie in Zeiten günstiger Aussenbedingungen oft höhere Leistungen als diese erzielen. Innerhalb der Getreidearten ist die Gerste ein stabiler, Hafer ein mehr labiler Typ; Weizen nimmt eine Mittelstellung ein.

Um die kausalen Ausstrahlungen des Wasserhaushaltes auf andere Funktionen zu untersuchen, ist der Vergleich sonst gleichartiger, aber durch Dürre-resistenz und Dürre-empfindlichkeit unterschiedener Sorten landwirtschaftlicher Kulturpflanzen geeignet. Dabei ergibt sich, dass innerhalb der artspezifischen Konstitution die resistente Sorte stets eine wirksamere Regulation der Wasserabgabe besitzt; diese ist wesentlich bedingt durch die höhere Empfindlichkeit und schnellere Reaktion der Spaltöffnungen bei ihren photischen und hydroaktiven Bewegungen. Damit wird eine bessere Stabilisierung des plasmatischen Wasserpotentials erreicht, welches die ausschlaggebende Bedingung für den geregelten Ablauf der gesamten Zellfunktionen ist. Bei seiner Herabsetzung im Tagesverlauf oder in Trockenperioden wird einerseits die Photosynthese erniedrigt und andererseits die Atmung erhöht. Weitere Dürreeffekte bestehen u. a. hinsichtlich der Nährsalzaufnahme, wobei die Aufnahme von K^+ vermindert, die von Ca^{++} und Mg^{++} vermehrt wird, und hinsichtlich der Ascorbinsäure, bei welcher sich Gesamtmenge und oxydierter Anteil steigern; das Redoxpotential wird so erhöht und das Gesamtzellgeschehen in Richtung der Dissimilation verschoben.

Letzten Endes beruht somit die Dürre-

resistenz auf Eigenschaften des Plasmas, genauer, seiner Struktur. Alle dürreresistenten Sorten zeigen gegenüber dürrerepfindlichen eine erhöhte Strukturviskosität. In Analogie zu den beim Schütteln von Pflanzen beobachtbaren Vorgängen treten bei der Entquellung des Plasmas mechanische Spannungen in der fibrillären Struktur auf, welche zu Zerreibungen führen. Diese bedingen, wie beim Schüttel-effekt, eine Vergrößerung der Maschenweite (Erhöhung der Permeabilität und Transpiration, Herabsetzung der Viskosität), die Freilegung polarer Gruppen (Erhöhung der Quellbarkeit und der negativen Überschussladung) und die Freisetzung hydrolysierender und dehydrierend-oxydativer Fermente (Erhöhung der Atmung); die Erniedrigung der Photosynthese beruht vermutlich auf Strukturstörungen in den Chloroplasten. Diese Dürrereaktionen gehen infolge der Ladungsabschwächung und des

geminderten $\frac{K^+}{Ca^{++} + Mg^{++}}$ -Verhältnisses in eine

Restitutionsphase über, in welcher die Wiederverknüpfung von Plasmafibrillen erfolgt und die Reaktionen sich wieder dem Anfangszustand nähern, ja über ihn hinausgehen können, weil manche Dürreeffekte, wie z. B. die Kationenverschiebung, längere Zeit nachwirken. Es entstehen dann abgehärtete Pflanzen mit der Reaktionsphase entgegengesetztem Verhalten. Reaktions- und Restitutionsphase sind deshalb beim Studium der Dürreeffekte wohl auseinanderzuhalten.

Discussion

CH. KILLIAN confirma l'absorption des ions, p. e. du calcium. Touchant la question de viscosité du protoplasme, il confirma la faible résistance à la desiccation.

H. R. OPPENHEIMER: The short weighing method is much older than assumed, it was established as early as in 1870.

H. WALTER: Es sind zwei Ansichten über Dürre-resistenz zu unterscheiden. Von landwirtschaftlicher Seite ist das Produktions-

problem wichtiger, ökologisch dagegen Fähigkeit ohne Schädigung des Sproßsystems zu überleben. Die Theorie von STÖCKER ist eine ausgezeichnete Arbeitshypothese.

H. WALTER (Hohenheim, Stuttgart)

Der osmotische Wert (die Hydratur) als Indikator der Wasserbilanz von ökologischen Typen in verschiedenen Klimazonen

Die Mitteilung bringt Ergebnisse der Forschungsreisen des Verfassers in Nordamerika und Afrika in der Zeitspanne 1929–1938.

Als Rockefeller Fellow am Desert Laboratory in Arizona fand Verfasser, dass für den Ablauf der Lebensfunktionen der „Wasserzustand“, die Hydratur, der Pflanze massgebend ist.

Als Mass der Hydratur dient die relative Dampfspannung (Feuchtigkeit) oder bei den höheren, eigenfeuchten (homoiohydran) Pflanzen der osmotische Wert des Zellsafts, durch den der Plasmaquellungszustand mitbestimmt wird.

Bei optimaler Wasserversorgung besitzen die Blätter einer jeden Pflanzenart einen bestimmten, charakteristischen osmotischen Wert (W_{opt}). Eine Verschlechterung der Wasserhältnisse führt zum Anstieg der Zellsaftkonzentration bis zu einem maximalen osmotischen Wert (W_{max}), bei dem irreversible Schäden an den Blättern eintreten.

Die Spanne $W_{opt}-W_{max}$ kann bei den einzelnen Arten gross (euryhydre Arten) oder klein sein (stenohydre Arten). Der Anstieg des osmotischen Wertes bei erschwerter Wasserversorgung erfolgt bei hydrolabilen Arten rasch, bei hydrostabilen, die ihre Transpiration frühzeitig einschränken oder ein leistungsfähiges Wurzelsystem besitzen, langsam. Die dürre-resistenten Pflanzen sind euryhydre hydrostabile Arten.

Verfasser hat in Europa, Amerika und Afrika viele Tausende von Bestimmungen des osmotischen Wertes ausgeführt. Ihre Auswertung zusammen mit den Untersuchungen anderer Autoren hat gezeigt, dass der osmotische Wert,

namentlich in ariden Gebieten, ein feiner Indikator für die Wasserbilanz ist und zur Charakterisierung der ökologischen Gruppen in verschiedenen Klimagebieten dienen kann.

Eine statistische Auswertung ist nicht zweckmässig, dagegen geben die osmotischen Spektra der ökologischen Gruppen eine gute Übersicht.

Solche werden gezeigt 1. für die Kakteenwüste in Arizona, die Prärie und die Rocky Mountains in Amerika, 2. für Mitteleuropa, das mediterrane Gebiet und die Steppen Vorderasiens sowie 3. die feuchten Tropen Afrikas. Dabei werden die Halophyten nicht berücksichtigt. Sie stellen einen Typus für sich dar.

Hydrophyten sowie Pflanzen feuchter Wiesen und Schattenpflanzen des Waldes sind steno-hydré, sehr hydrolabile Arten. Dagegen sind Sukkulente zwar ebenfalls steno-hydré, aber äusserst hydrostabile Arten. Malakophylle Xerophyten sind euryhydre Arten, sklerophylle Xerophyten sowohl euryhydre als auch hydrostabile Arten. Diese Grundtypen sind durch zahlreiche Übergänge verbunden, die an Hand der osmotischen Spektra im einzelnen besprochen werden.

In der Arizona-Wüste lassen sich z. B. durch die osmotischen Spektra unterscheiden: Stamm- und Blattsukkulanten, Winter- und Sommer-ephemere, Regengrüne, poikilohydré Farne, Malakophylle und mehr oder weniger extreme sklerophylle Xerophyten. Prärien, Steppen und Steppenheidepflanzen haben umso niedrigere Werte, je früher im Jahr sie ihre Entwicklung abschliessen oder je tiefer sie wurzeln; W_{max} wird nur in extremen Jahren erreicht. Alpine Arten sind sowohl in den Alpen als auch in den Rocky Mountains steno-hydré Arten, während die immergrünen Bäume und Zwergsträucher der subalpinen Stufe im Winter häufig sehr hohe Anstiege der Zellsaftkonzentration aufweisen. Arten der feuchten Tropen sind extrem steno-hydré Arten mit niedrigen osmotischen Werten und oft ziemlich hydrostabil.

Literatur

H. WALTER, Einführung in die Phytologie 1: 326–356, 3: 109–332, Stuttgart (Ludwigsburg) 1950.

Discussion

CH. KILLIAN: Les valeurs osmotiques des racines de plantes méditerranéennes montrent une ascension excessive au moment du dépérissement et valeurs inférieures pendant toute la période végétative.

F. RAWITSCHER had a question on the osmotic values of roots.

H. R. OPPENHEIMER (Rehovot)

Summer Drought and Water Balance in the Near East

Studies on the water relations of plants were initiated in Palestine about 25 years ago, where climatic conditions are extremely favourable for the study of drought effects and drought resistance. The available data and publications warrant the following conclusions:

1. During the long and dry summer, some plants reach very high figures of transpiration. In the almond a maximum of 3445 mg per gram of fresh weight per hour has been found. Desert plants like *Haplophyllum* and irrigated crops like maize and *Citrus* also use water rapidly if the water supply is good.

2. Plant groups of different average transpiration intensities can be distinguished: a) Deciduous trees with often ring-porous wood show a high water utilisation in contrast to sclerophyllous maqui shrubs and conifers. b) Mesomorphic desert plants as *Haplophyllum* and *Heliotropium* use more water per unit fresh weight, if well supplied with moisture, than succulents, such as *Salsola* or *Suaeda*. Thus, in spite of the fallacy of the transpiration criterion for the distinction between xerophytes and mesophytes, the distinction of types of different average water use and requirement seems fully justified, and highly important for agriculture and forestry.

3. Various means are used to maintain a balance between water-loss and absorption. Deep penetrating roots absorb ground-water and that present in soft rocks with a high water storage capacity. The depth of the soil

cover, the arrangement of stratified layers in rocks, the presence of fissures and pockets in the bed rock are therefore important for plant life, as the width and depth of root penetration and other rooting habits of the various types of xerophytes inhabiting the region. Types storing water are remarkably rare and true succulents are found mostly in salty desertic localities. But wide use is made of the reduction in number and size or the complete shedding of leaves, especially in deserts. On the other hand the closure of the stomata in xeromorphic leaves has been found extremely effective in maqui as well as in desert vegetation, often cutting water-loss down to nearly zero. Dew absorption is sometimes important.

4. Death of perennial plants by desiccation (except in seedlings) is rarer than would be presumed. But cases of an adverse water balance are rather frequent, and the region abounds in plants able to endure high water deficits reaching 75 per cent in leaves of *Haplophyllum*, about 66 per cent in *Rosmarinus* and over 70 per cent in unirrigated *Citrus* trees, before the leaves die off. On the other hand, osmotic values rise sometimes to 40 or 50 atmospheres in maqui as well as in desert plants. Still higher figures are rare, even in deserts, and occur mainly in salt marsh vegetation. It seems that "high-pressure plants" exploiting water unavailable to other plant species from the same drying soil layers are rather rare.

5. Plants enjoying supply of abundant water from ground-water layers, soils or rocks often surprise even after prolonged drought by low saturation-deficits and low osmotic values in spite of very high water-losses. The others are obliged to economize water either suffering high deficits or not, and various degrees of stomatal and other restriction are observed.

6. In general, we observe that even in the driest localities the organisms are well adapted to the conditions of their natural surroundings. Even in deserts, plants open their stomata if struck by the sun rays, at least for some time in the morning, though the water reserves are much restricted. The resulting transpiration

curves continuously decreasing after a high peak in the morning are highly characteristic for conditions of high strain, but before the onset of extreme want and starvation. Damage by overheating has been found to be rare in natural habitats (maqui).

Discussion

A. HEILBRONN erbittet Auskunft über die Resistenz-Einrichtungen der flachwurzelnden *Peganum Harmala* und beschreibt eine bisher unbekannte xeromorphe Einrichtung, die sich bei *Onobrychis argyrea* findet: Deckhaare, die sich bei Trockenheit über die Stomata legen und in feuchter Luft sich erheben und die Stomata freilegen. Der Bewegungsmechanismus ist doppelt gesichert: Solange das Blatt jung ist und die Haare noch leben führt Turgorsteigerung einer Zelle mit Hebelwirkung zur Aufrichtung,

Nachlassen des Turgors zur Senkung der Haare. Nach dem frühen Absterben der Haare führt eine hygroskopische Torsion zum selben Ziel.

CH. KILLIAN rappelle les observations de THODAY sur les fougères reviviscentes, il signale du tannin dans les cellules de plantes du Fouta Djallon résistant à la chaleur (*Notochlaena lanuginosa*, *Salacia guianensis*), et il fait mention d'un champignon endophytique non mycorrhizant chez *Polycarpaea corymbosa*, plante humicole des dalles latéritiques.

Bezugnehmend auf die Bemerkung von A. HEILBRONN über *Peganum Harmala* fragt F. RAWITSCHER nach dem Wassergehalt des Bodens in der betreffenden Tiefe.

M. ZOHARY: *Peganum Harmala* does not resist in the deserts of Palestine during the summer and therefore cannot be considered a xerophyte.

H. VAN VLOTEN had questions relating to mycorrhiza and root development in *Pinus pinea*.

SESSION 4

July 17th, 9 a.m. — noon

Chairmen: BROR PETTERSSON and R. F. DAUBENMIRE, Recorder: L.-G. ROMELL

SUBJECT:

Dissemination and Colonization

BROR PETTERSSON (Helsingfors) *An Experimental Investigation of the Dispersal of Mainly Anemochorous Nordic Phanerogams*

Settling velocities of diaspores in air were determined for species belonging to the following genera: *Typha* (2), *Phragmites*, *Melica*, *Calamagrostis* (2), *Eriophorum* (2), *Scirpus*, *Populus*, *Salix* (4), *Clematis*, *Dryas*, *Trifolium*, *Epilobium* (8), *Chamaenerium*, *Cynanchum*, *Valeriana*, and a fair number of pappus-equipped *Compositae*. More than one hundred diaspores were used for the test in every case, making a total of some 17 000 determinations.

The results obtained show that the floating capacity of some anemochorous diaspores has been greatly overestimated. A seemingly excellent flotation equipment of the diaspores is no indication of an equally high floating capacity. *Populus*, *Taraxacum* and *Hypochaeris* afford convincing examples.

It was calculated that one diaspore in a million will reach the following distance with a wind of 10 metres a second.

<i>Chamaenerium</i>	29	kilometres
<i>Epilobium adenocaulon</i>	23	"
<i>Salix caprea</i>	18.6	"
<i>Typha latifolia</i>	16.4	"

<i>Populus tremula</i>	5.4 kilometers
<i>Taraxacum microlobum</i>	3 "
<i>Hypochoeris maculata</i>	1.5 "
<i>Taraxacum balticum</i>	0.9 "
<i>Leontodon autumnalis</i>	0.7 "
<i>Clematis sibirica</i>	0.5 "
<i>Melica ciliata</i>	0.5 "
<i>Trifolium arvense</i>	0.3 "

Included in this list are examples of very good as well as of surprisingly poor floating capacity.

The same diaspores as tested for floating power in air were tested for buoyancy in water either fresh or brackish or salt. The effect of transfers from fresh to salt or from salt to fresh water was also studied. Lots of one hundred to a thousand diaspores were used in the tests. Sunken diaspores were counted every 12 hours, and average floating times were computed from these data. In some species, seedlings developed during the experiments and were included in the tests. The remaining diaspores, whether floating or not, were tested for germinating capacity.

Discussion

R. F. DAUBENMIRE: Our interest in probability of long-distance dispersal is stimulated by search for explaining exceptionally large steps in migration, so it is natural to lay much emphasis upon very low probability. However, we should discount mathematical probabilities somewhat for the fact that these light-weight disseminules within a species which increase the probability of long dispersal are disseminules with below-average food reserves and therefore rather poorly equipped to meet competition where they alight.

K. FÆGGI: The introduction of more complicated formulas for average dispersal is of little use as the parameters are on the whole not sufficiently well known to warrant the use of the formulae.

H. A. HYDE: SCHMIDT's formula on Austausch has been revised later by SUTTON. PETTERS-

SON's figures might well be revised with advantage in the light of SUTTON's calculations.

L.-G. ROMELL: Distances of dispersal may come out much too low from averages and SCHMIDT's formula, which fails to account for differences between low and higher levels as to size of eddies, strength of upward currents and velocity of wind.

N. POLUNIN: Whereas none would deny the importance of studying means and modes, we must not forget that extremes are nevertheless of great interest and often fundamental importance in these connections. Thus, for example, phytogeographers must always remember that for successful establishment of a taxon in a new area a single disseminule in a millenium may suffice.

NICHOLAS POLUNIN (Montreal)

made the following statement about his paper on Seeking Airborne Botanical Particles about the North Poles:

Mr. Chairman, Ladies and Gentlemen:

Some of you may have attended the Palynological Foregathering last week at which I had, most reluctantly, to make a sad little speech of apology and explanation for disrupting the programme by not being able to give the paper which I had prepared for that occasion. The same unfortunate situation holds today—indeed with more force. To obtain certain facilities for my work I have latterly had to seek Government support, which not unnaturally involves the responsibility of submission of results to the gubernatorial body. All papers so concerned have to be 'cleared' before publication. On receiving Professor Romell's honouring invitation to address you on this occasion, I consulted the office concerned and was encouraged to prepare the paper, at which I subsequently worked happily for weeks. But the bureaucratic machine would not release it, and the same fate befell that prepared for Dr. Erdtman. Even a series of cables from our Congress President and diplomatic friends have failed to

dislodge these papers or obtain permission for me to give talks or submit abstracts on the subjects concerned. And during the past few days I have sought clearance to give you a different paper, which has nothing to do with the North Pole or any recent flying or other things I have been doing or may plan; but that too has just been refused in a cable I received during the weekend. Presumably we may blame the state of the world. Anyhow I feel at least in honour bound to keep entirely off the subject; and whether or not I shall be able to publish any more of this work must remain to be seen. Meanwhile to you, Ladies and Gentlemen, I must express my profound regret as well as keen personal disappointment at not being able to give you any paper or further details whatsoever.

Instead of Professor POLUNIN's paper, the following paper was read, which had been scheduled for Section PHG of the Congress.

KNUT FÆGRI (Bergen)

On Long-Distance Pollen Transport

The problems of long-distance pollen transport were seriously discussed from a pollen-analytic point of view during the early days of pollen analysis. As, however, experience showed that this source of error was generally not of any significance in ordinary pollen-analytic work, it has on the whole been neglected. Only in Arctic areas does the long-distance pollen play a more prominent part in the pollen rain. Recent experience in recording pollen rains over the sea have shown that pollen grains are regularly transported very long distances, even if the quantity is negligible as compared with the local pollen production and sedimentation. As pollen grains are in principle not very different from the air diaspores of most cryptogams, the observations of recent long-distance pollen transport are of great significance for the discussion of phytogeographic relations. In pollen analysis long-distance pollen constitutes a serious obstacle when it comes to decide

about the first immigration of species. Very painstaking analyses can serve to solve the problem.

Discussion

H. A. HYDE: The catch of oak pollen at Bergen might well have been much higher in some years since this species in Britain has a pollen-production periodicity of one year in five and 1949 was not a bumper year. Observations on atmosphere pollen made at Cardiff suggest that at times elm and pine pollen caught out of season may have been blown across the Atlantic.

A. S. THOMAS: The importance of wind dispersal may be underestimated by those who have not experienced tropical conditions, where the winds are not constant and have much turbulence. I retell the case of sheets of collecting paper carried off by a whirlwind, and of the sudden appearance of the fungus *Hemileia vastatrix* on coffee in Ceylon, probably from wild coffee in Africa.

L.-R. ROMELL referred to MALMSTRÖM's catches of pollen of pine and spruce far north of any pine or spruce flowering at the time and asked for Professor FÆGRI's opinion on the "tail" of spruce pollen found in deeper strata of the bogs, once a point of dispute between HESSELMAN and VON POST.

K. FÆGRI: HESSELMAN and VON POST were both right. The immigration or, as the case may be, absence of a species can in many cases not be decided by means of pollen analysis alone. One must take into account the whole geographical and biological history of both the species and the area in question.

ELSIE CONWAY (Glasgow)

Studies in the Spread of Bracken

The increase of *Pteridium aquilinum*—the common bracken fern—has become so great in certain regions of high rainfall in Great Britain that it has now affected the established flora and become an agricultural pest. Its

spread is mainly vegetative, but the increase, even under controlled conditions, has been greater than is compatible with former ideas of sparse frond production at the rate of one frond per branch per year. Further work has become necessary on the methods of growth and the mode of invasion by the plant; and these have been carried out with special reference to conditions in the West of Scotland.

It is clear that entirely new infections of the plant must come from sporeling colonies, though, generally, these are infrequently found in the field. The appearance of large numbers of such colonies on bombed areas, and their spread, proves that, under suitable conditions, spore development can effect a rapid increase of the plant. Thus, the problem of invasion has been examined in relation to the factors affecting sporing and sporeling development, and those affecting rhizome and frond-bud development in the adult sporophyte, and it is now suggested:

a) that the spore output and germination rate are potentially high, but that the prothallus is a vulnerable organ reacting sharply to climatic and other factors. In comparison with the number of spores shed, few sporophytes develop in the field.

b) that each young plant which becomes established is capable of rapid and marked growth, since the sporophyte is much more tolerant than the gametophyte. The dorso-ventral, underground rhizome has great powers of development, and a single spore may grow into a well-set colony in its first summer and become a definite invasion by the end of the second year. The earlier ideas of bud formation are no longer acceptable.

Discussion

J. TENGNÉR: In Swedish forests, where the bracken fern is a common weed, especially on clear-felled, burnt or otherwise cleared areas, the plant seems to propagate mainly vegetatively.

In more closed stands subterranean stems are often much more abundant than may be thought from the sparse occurrence of fronds. The dwarf shoots of the subterranean stems may carry but few and rather small fronds and yet be provided with a varying number of sleeping buds, ready to develop under the favourable conditions following fellings. This fact would in part explain the rather fast spread of bracken in cleared areas.

R. E. HOLTUM: In Malaya, as in Britain, sporeling plants of *Pteridium* are rare. By contrast, sporelings of the thicket-forming *Gleichenia* are very abundant. This is perhaps connected with the fact that the *Gleichenia* rhizome is slender and superficial so that it is more vulnerable and the plants are killed by one cutting or burning, whereas *Pteridium* is not killed by one such cutting or burning.

A. S. THOMAS: The range of soils on which *Pteridium aquilinum* grows are similar in Africa to those mentioned by Dr. CONWAY. In places where the soil is very leached and acid, bracken is replaced by thickets of *Gleichenia*.

N. POLUNN asked about controls of this pestiferous nuisance which is so appallingly widespread and aggressive. He has seen it swamping and killing *Ulex* bushes 6 feet high, and other plants in America in a similar manner.

LUCY B. MOORE: In New Zealand starch extracted from bracken rhizomes formed an important article of diet for pre-European Maoris. Wild pigs feed extensively on bracken rhizomes. The account of bracken agreed in many respects with observations made in New Zealand on *Paesia scaberula* which has thin superficial, not thick subterranean rhizomes. There prothalli of both *Paesia* and bracken can be found in the field.

L.-G. ROMELL: The case of bracken, as given by Dr. CONWAY, has a very general interest by strikingly illustrating the difference between the dispersal of seed, or other disseminules, and the spread of a species. The difference is a fundamental one and yet is not always realized.

SESSION 5

July 17th, 1—4 p. m.

Chairmen: W. H. PEARSALL and R. F. DAUBENMIRE, Recorder: L.-G. ROMELL

SUBJECT:

Grazed Lands

W. LÜDI (Zürich)

Experimental Investigations into the Sub-Alpine Nardetum

The pasture association of *Nardus stricta* (Sieversii-Nardetum strictae) has an extremely wide range in the sub-alpine region of the Swiss Alps. It consists of acidiphilous plants, most of them forage weeds, and indicates a poor and acid soil. The production of forage is very poor. Experiments have been made in a typical pasture Nardetum at Schinigeplatte near Interlaken (1950 m above sea-level) during the last 20 years to examine the conditions leading to the formation of the Nardetum-sward and the possibilities of improving the composition of this poor grass land. The soil which was deep, loamy and not poor in nutritive substances but very acid (pH 4.5) was treated with several mineral manures, stable manure, and compost. In some experimental series there was every year manuring and cutting, in others manuring every 2, 4 and 6 years and then cutting without manuring to observe the after-effect of manuring. The same experiments were made on the old Nardetum sward and on cleared ground with or without sowing a mixture of good forage plants and weeds.

It was also determined what effect burning or neutralizing the soil (to pH 5.5 or 7) had on the formation of a new sward. Every experiment was replicated 5 times using plots one metre square arranged in mosaic manner, each surrounded by a border 30 cm wide receiving the same treatment as the plot itself. There were, in all, 18 different series of experiments and 350 experimental plots.

The experiments showed the extreme plastic-

ity of the Nardetum sward. A complete manuring (NPKCa or stable manure) changed the low, weedy Nardetum within 2–3 years completely into a high forage meadow with dominant forage grasses (*Festuca rubra* ssp. *commutata*, *Phleum alpinum*, *Agrostis capillaris*). The crop was 5 times bigger or more and the weeds disappeared. Incomplete manuring had a smaller but often a very decided effect. NPK had a good effect in the first years and then came a quick degeneration of the meadow. N favoured *Nardus*, P favoured in the first years the development of Leguminosae and then the effect decreased. The effect of K was hardly to be observed. CaCO_3 had a slow effect, improving from one year to the other (exchange of bases, slow neutralisation of the soil). It was extremely interesting to observe the reactions of the different species. Some were favoured, others damaged by Ca, N and P and combinations of them. Some so-called "acidophytes" developed very well with manuring but were effaced by competition. After sowing the sward was always an association of good forage plants, but without manuring it remained dwarfish and degenerated slowly. But a Nardetum was never formed directly.

Discussion

H. WALTER: Diese Versuche sind ausserordentlich wichtig, weil der Konkurrenzfaktor nicht ausgeschlossen war. Eine Unterdrückung erfolgt meist durch Konkurrenz mit anderen, stärker wachsenden Arten.

F. R. BHARUCHA: In experiments made in India, potassium not only had no positive effect but actually depressed the yield of grasses.

H. B. GILLILAND (Johannesburg)

The Experimental Investigation of Grass Communities on the Witwatersrand University's Field Research Station Frankenwald at Johannesburg, South Africa

The Witwatersrand is a westward arm of the Transvaal Plateau (the Highveld) forming a ridge parallel with the Magaliesberg Range but further south. It is the watershed between the Limpopo and the Vaal Rivers and lies between 4500 and 6000 feet. Frankenwald is situated on the north face and it is interesting to reflect that at 26° S latitude and 28° E longitude it occupies approximately the same position in the Southern hemisphere as Luxor in Egypt in the northern. The soil is a sandy loam derived from the Older Granite and has a pH ranging from 4.5 to 5.2. The region is one of summer rainfall (1) with the most difficult period for plants in the winter season which is dry, sunny and with wide diurnal fluctuations of temperature, frosts being common at night. WEINMANN's work (2) suggests that this results in an annual migration of food reserves from the aerial to the subterranean portions of the plants in winter. Not infrequently the spring rains fail so that winter is capped with an arid period of drought coupled with rising temperatures.

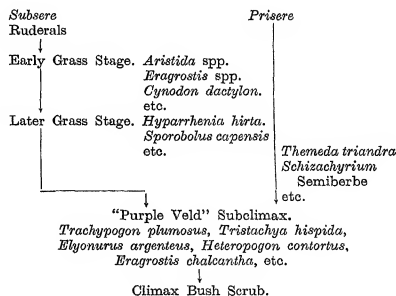
Although there are undoubtedly more urgent problems in South Africa, such as the advance of the Karoo desert, a menace comparable to the American dust-bowl experience (3), Frankenwald, lying in typical South African pastoral country, is concerned primarily with the management of vegetation as the basic food supply for the grazing animals in these more northern latitudes of the Union for beef and milk production.

Many workers have, over the past 15 years, tackled problems relevant to this theme including light and temperature relations (4), the effect of fire (5), the interrelationships of termites and vegetation (6), insect populations (7), soil fungi (8), and community changes following from various rates of stocking (9, 10).

Perhaps the most interesting result which has developed, however, is that which has arisen from the application of nitrogen, in the form of artificial fertiliser, to a sub-climax grassland community whose carrying capacity has been measured in terms of lbs. of beef. The community has changed until it is now dominated by species which normally occur in the early stages of the subere.

The vegetation of Frankenwald is a bunch grassland fire subclimax of wide occurrence over the western portion of the Witwatersrand. The climax is represented by several relic communities of scrub and bush (11, 12, 13) some of which, especially in more sheltered gullies, may well be post-climax. These are poorly represented on Frankenwald. Successional stages in the development of the vegetation have been studied (14, 15) and the subere clearly demonstrated.

In diagrammatic, simplified form it can be represented thus:



Considerable attention has been paid to methods and techniques. The conclusions concerning succession are therefore based on careful quantitative study (16, 17, 18).

Improvements in yield following the application of artificial fertilisers have been studied by a variety of methods. Clipped quadrates were used and reported on as a method of estimating not only yield but chemical composition (19). MEREDITH and HALL and co-workers reported

very fully on the changes in carrying capacity resulting (20, 21, 22). "Cow-days" or "grazing days" as a method of measuring production were soon found to be unsatisfactory and a weighbridge was installed. The results could then be measured in terms of pounds of live weight.

The most satisfactory improvement, in terms of production, resulted from the application of annual dressings of nitrogen, phosphorus and potassium in which the nitrogen was applied at the rate of 600 lbs. ammonium sulphate per morgen in three dressings of 200 lbs. each in spring, midsummer and early autumn. It was shown that over an 8 year period this was equivalent to 133 $\frac{1}{2}$ lbs. N/morgen/annum (22). Neither the phosphorus nor the potash appear to affect the result markedly. Currently the experiment continues with the substitution of milk production from a selected group of Frisian cows as the measure. The aim of improving the carrying capacity has been achieved and it is claimed (22) that it has proved economic.

However an interesting change in the grass community occurred in six years (23) in an experiment laid out in "purple veld" of the normal composition with *Trachypogon plumosus*, *Tristachya hispida*, *Heteropogon contortus*, *Elyonurus argenteus* and *Eragrostis chalcantha* as the prominent species. The change that had occurred was found as follows after a further 10 years (22).

Table 1.

Composition of grassland of "A" series at Frankenwald at commencement of experiment in 1933 compared with composition in plots of that series which had received heavy nitrogenous artificial fertiliser dressings, analysed in 1949.

Grass	% 1933	% 1949
<i>Trachypogon plumosus</i>	1.54	0.6
<i>Tristachya hispida</i>	1.45	1.4
<i>Heteropogon contortus</i>	2.51	0.0
<i>Elyonurus argenteus</i>	2.37	0.0
<i>Eragrostis chalcantha</i>	2.39	0.0
<i>Digitaria tricholaenoides</i>	2.08	1.9
<i>Brachiaria serrata</i>	0.71	0.0

Grass	% 1933	% 1949
<i>Harpechloa falx</i>	0.62	2.9
<i>Themeda triandra</i>	0.26	0.0
Other grasses	3.91	5.2
<i>Eragrostis</i> spp.	0.00	17.7
<i>Cynodon dactylon</i>	0.00	0.5
Non-Grasses	0.68	0.9
Total Cover	18.52	37.0

In essence the early subseral *Eragrostis* spp. now dominate the land although the production and carrying capacity are maintained and the basal cover has improved. The root systems of the principal grasses involved gave no clue (24). There are indications that the same community may result from the application of the same fertiliser to the early subseral stages directly, and that grazing is not an important factor in the change. Intensive studies of the *Eragrostis* spp. concerned have commenced, more especially as they appear to seed freely and it may therefore be possible to develop a sown pasture. A complementary search for a suitable companion legume has also commenced.

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Discussion

F. G. RENNER: The speaker mentioned that the area described was a shrub climax, but that in its present condition the scrub growth had given away to bunchgrass. In the United States this is extremely rare—unless man has interfered with the natural succession. It would be of great interest to know what the factors are that have changed a scrub climax to bunchgrass.

H. WALTER: Phosphor hatte keine Wirkung, und doch sind die Böden in Afrika sehr arm an Phosphor. Ist der P-Gehalt der Böden höher am Witwatersrand?

H. B. GILLILAND: It is surprising that the effect of phosphorus was so small.

F. G. RENNER (Washington, D.C.)

Experimental Studies on Natural Grazing Lands of the U.S.

Selected studies of the effects of climate, fire, and grazing on natural grazing lands are reported.

The severe drought of 1933-1939, and the following years of more normal conditions disclosed significant changes in the Prairie vegetation. The greatest change was the reduction of the midgrasses, and the accompanying extension of the shortgrass type. These changes were directly related to the differences in the root system, the longer-rooted midgrasses being able to penetrate below the four feet of dry soil to reach needed moisture. Recovery following drought was more rapid in the shortgrass type, despite the loss of nearly three-fourths of its basal cover. The midgrass type lost only half

of its basal cover. Because of the slower recovery of the midgrasses, their greater forage production, and the fact that the composition of the vegetation was changed so drastically, the economic losses from drought were far greater in this type. Soil moisture was the most important environmental factor, emphasizing the need to leave more unused forage to build up a mulch layer and increase moisture infiltration. The studies also furnished other valuable clues to management practices needed during and following drought conditions.

The use of fire to improve Kansas bluestem pastures has long been a controversial practice. Many land owners have considered burning necessary to insure even the full use of the forage the following year, to improve the quality of the forage, and to stimulate earlier growth. A five-year ecological study provided the first available facts on this practice. Fall burning and early spring burning were detrimental. Late spring burning showed two advantages, greater leafiness and higher protein content of the new growth, and earlier growth due to higher soil temperatures on the burned areas. The yield was 12 per cent less, however. Burning in the fall and early spring resulted in respective reductions in the forage yield of 39 and 33 per cent, with no advantages.

On semi-arid ranges of the United States, black grama was found to be a dominant constituent of the vegetation. Because it was also highly relished by livestock, the degree to which it was grazed determined whether the range would be maintained, improved, or become seriously depleted. Studies to determine the intensity of grazing this plant would withstand showed that it was unsafe to remove more than 50 per cent of the forage, by weight, if the black grama was to be maintained. Grazing beyond this point sharply reduced the forage yield, stimulated the invasion of poorer plants, and induced accelerated wind and water erosion. On ranges that had been depleted by past overuse and drought, it was necessary to leave 65 per cent of the current growth to achieve improvement.

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Discussion

A. S. THOMAS: In Africa, burning definitely stimulated the growth of many grasses and was essential for the control of thorny shrubs which ruin so much of the African grasslands. There is evidence that burning or the spreading of ashes on the soil stimulates nitrification. Rain-fall figures may not give any guide to the supply of water in grassland for, in the absence of frost, the surface may be so compacted that the rain may never penetrate more than about a quarter of an inch below the surface.

W. A. ALBRECHT and L.-G. ROMELL both had questions on the reported decrease in yields following burning.

W. A. DAYTON (Washington, D. C.)

Range Management Research of the U. S. Forest Service

"Range," as used in the United States, is native forage-producing land, and occupies about 950 million acres, or about half the total land area of the country. Three-fourths of these ranges are in the West. About two-thirds are privately and one-third publicly owned. Most of the western range has an average annual precipitation of under 15 inches, with poor soil and rough topography; much of it is badly overgrazed. Four-fifths of this range area is important in water-production; about 350 million acres contribute silt disturbingly to major western streams, dams, and reservoirs. Nearly 75 per cent of the nation's sheep and goats, over half of its beef cattle and large numbers of other

livestock and wild game are supported on range at least part of the year.

Many problems of land management and of correlated uses are raised by range lands. Range research in the U. S. Forest Service was started in 1907 by the appointment of two technical men in the old Branch of Grazing, Drs. JAMES T. JARDINE and ARTHUR W. SAMPSON. This work now heads up in the Division of Range Research, headed by Mr. WILLIAM R. CHAPLINE of the Washington office, with subordinate divisions of range research in eight of the forest and range experiment stations in the field, under some of which are experimental ranges. Forest Service range research has developed better methods of handling range livestock and range lands, as in the bedding-out system of handling sheep and the deferred and rotation grazing systems. It is concerned also with many other phases, including artificial reseeded, better distribution of livestock by watering, salting, fencing, and riding; proper utilization; proper seasonal use; range readiness;

eradication of poisonous and other undesirable plants; range plant succession; relation of livestock grazing to other uses such as timber, recreation, and wildlife; the life history, physiology, phenology, distribution, and economic values of native range plants, etc. The literature on these and related subjects is now very extensive. Among the more outstanding publications are: JARDINE & ANDERSON's "Range management on the national forests"; SAMPSON's "Natural revegetation of range lands based upon growth requirements and life history of the vegetation"; CHAPLINE's "Range research in the United States" (published in *Herbage Reviews*, 1937); and the Forest Service's "The Western Range" and "Range Plant Handbook."

Discussion

Questions on methods of reseeded and technique of investigation were asked and answered.

SESSION 6

July 18th, 8.30 a.m. — noon

Chairmen: R. COMBES and P. CHOUARD, Recorder: L.-G. ROMELL

SUBJECT:

Problems of Adaptation

The session opened ahead of the scheduled time to accommodate the paper next following, which was not on the Section's program.

P. A. BARANOV (Moscow)

Cultivated Plants in Extreme Conditions in the Pamirs

In order to make a thorough study of the biology of the plant in extreme conditions of life, the Academy of Sciences of the USSR has organized the Pamirs' Biological Station which is located 3860 metres above sea level. The report contains data of the studies of this sta-

tion pertaining to the adaptability of cultivated plants to the severe conditions of the Pamirs.

Alpine conditions are stimulating the physiological processes and the activity of metabolism in the plant goes sharply up. Thus the activity of the photosynthesis during the warm hours of the day exceeds several times that of the flatland conditions and amounts to 150 mg CO₂ per 1 square decimetre in an hour. A characteristic feature of the metabolism in the

cultivated plants raised in the Pamirs is the accumulation in their cells of an extremely large amount of sugar (in cereals up to 35–40 per cent, in the leguminous plants up to 18–20 per cent of their dry weight). This creates a physiological basis of a sharply rising frost resistance of the plant. Most of the types studied stand night frosts from -15° to -22° . Even potato plants stand a temperature of -9° . Many cultivated plants considerably increase their content of vitamin "C". The anatomic structure of the plant undergoes important changes. The specific gravity of the meristem in the body of the plant grows, the cells cling closer together, the amount of woody tissues goes sharply down, etc.

The cultivated plants of the xerophyte type possess the best capacity for adaptation under the new, severe conditions and for the completion of their ontogenesis.

The study of changes occurring in a plant in the course of several generations has given us an opportunity to establish the formation of adaptive peculiarities and serves as an illustration for the assertion pertaining to the directed changeability of an organism in a new environment.

The Station has in the course of its work accumulated types and groups of plants suitable for the cultivation in the Pamirs and these types and groups are being made use of in practice.

Discussion

There was a fairly lively exchange of views, although records are left only of the following remarks and queries.

J. LEVITT: Were the low temperatures survived by these plants air temperatures or plant temperatures? Since these temperatures change so rapidly, do the plants freeze or do they undercool? When plants are transported to the high altitudes, do all individuals become adapted or are some killed by frost and only the surviving ones used to plant next year's crop?

H. R. OPPENHEIMER: Many generations are needed for drawing safe conclusions.

G. DELOFFRE: Vers 1920, les chercheurs du laboratoire de Buitenzorg ont montré que des changements d'altitude permettaient d'accroître la résistance à certaines maladies et en particulier de lutter contre la maladie du Seré de la Canne à sucre.

I. REICHERT asked whether the property of oozing out oil drops was maintained also when the same plants were brought back to lowland.

R. COMBES (Paris)

Le mécanisme d'action du milieu extérieur sur la forme des végétaux

C'est au cours du siècle dernier, entre 1809 et 1878, que furent découvertes les grandes lignes du mécanisme d'action des facteurs externes sur les organismes: action directe sur le fonctionnement physiologique, action du fonctionnement physiologique sur la construction physicochimique des tissus, action de cette dernière sur l'élaboration des formes. Ainsi étaient reconnues les trois parties d'une chaîne de phénomènes qui relie l'action du milieu ambiant à la morphogénèse.

Ce furent d'abord les conséquences morphogéniques de l'action du milieu qui furent abordées par l'observation, puis par l'expérience. Ensuite furent mis en évidence un certain nombre de faits précis relatifs à l'action du milieu intérieur sur la morphogénèse. Ce n'est que plus tardivement que fut entreprise l'étude des deux premiers maillons de la chaîne: action du milieu extérieur sur les grandes fonctions et de celles-ci sur le milieu intérieur. Alors seulement put être tentée une explication complète du mécanisme d'action des facteurs externes. En 1892 STANGE en donne une relative à l'action de la concentration du milieu. Plus tard les travaux de ROSÉ, de plusieurs de mes collaborateurs et de moi-même, complétés par ceux de KONINGSBERGER, de BÜNNING, de KÖGL, de LARSEN sur les auxines, permirent une explication du mécanisme d'action de la lumière. Les actions de deux milieux naturels complexes, climat

alpin et milieu aquatique, ont également été examinées dans leur ensemble.

Les plus grandes difficultés surgissent lorsqu'on parvient au contact des phénomènes de morphogénèse, à l'articulation des deux chaînons: milieu intérieur et construction des formes. J'ai tenté récemment, avec deux de mes élèves, en opérant avec les milieux aquatique et aérien, d'aborder l'un de ces problèmes, recherchant les causes qui peuvent expliquer les différences existant entre les espèces au point de vue de l'intensité de leurs réactions morphogènes vis à vis des facteurs externes. Les résultats obtenus jusqu'ici montrent que les espèces à faibles réactions morphogènes ne diffèrent de celles à fortes réactions morphogènes ni par la sensibilité de leur fonctionnement physiologique aux facteurs du milieu ambiant, ni par celle de leur métabolisme, mais par l'intensité des réactions de leur morphogénèse vis à vis du milieu intérieur. C'est là un résultat qui localise le problème sans prétendre le résoudre.

Discussion

P. CHOUARD: *Lysimachia Nummularia*, réagissant morphologiquement si peu à l'eau ou à l'air, répond au contraire de façon intense au photopériodisme: elle est à entrenoeuds courts et à feuilles tassées et épaisses en jours courts. Ce serait un bon matériel pour éprouver les relations entre biochimie et morphogénèse.

G. NOACHOVITCH contribuera à la discussion à propos de la conférence de M. CHOUARD.

E. BÜNNING (Tübingen)

Umwelt und pflanzliche Eigenrhythmik

Die Pflanzen sind einem bestimmten Klima nicht nur dadurch angepasst, dass die Durchschnittswerte von Licht, Temperatur usw. des betreffenden Klimas für ihre Entwicklung optimal sind, und dass sie die extremen Werte vertragen. Vielmehr sind die Pflanzen, und zwar durch endogene jahres- und tagesperiodische Schwankungen ihres physiologischen Zu-

standes, auch den Jahres- und Tagesschwankungen der äusseren Faktoren angepasst.

Die endogene Tagesrhythmik ist für die Anpassung an die Tageslänge wichtig, weil sie die Grundlage für die photoperiodischen Reaktionen darstellt. Diese endogene Rhythmik besteht in einem physiologisch selbst gesteuerten Abwechseln einer sogenannten photophilen und einer skotophilen Phase. Für eine optimale Blütenbildung braucht die Pflanze während der photophilen Phase Licht, während der skotophilen Dunkelheit. Diese physiologische Rhythmik ist zwar endogen, aber die zeitliche Lage der Phasen kann durch Lichtreize bestimmt und verschoben werden. Die Gesetze dieser Regulierung sind uns weitgehend bekannt. Das unterschiedliche Verhalten von Kurz- und Langtagpflanzen lässt sich durch die Tatsache einer unterschiedlichen Regulierung der endogenen Tagesrhythmik durch Lichtreize vollständig erklären. Photo- und skotophile Phase sind oft äusserlich an Blattbewegungen erkennbar. Wesentlicher aber ist, dass sie auch durch unterschiedliche Fermentaktivitäten gekennzeichnet sind.

Es ist möglich, das Vorhandensein einer endogenen Tagesrhythmik durch Selektion zu erklären.

Manche ökologische Besonderheit, wie z. B. die Beschleunigung des Blühens im Hochgebirge, lässt sich durch bekannte Beeinflussungen der endogenen Tagesrhythmik durch äussere Faktoren, namentlich durch Einflüsse der Temperatur erklären.

Auch die endogene Jahresrhythmik ist auf der Grundlage von Selektionsvorgängen erklärbar. Es gibt noch zahlreiche Pflanzen, bei denen diese langperiodischen inneren Rhythmen in ihrer Periodenlänge stark von der Dauer des astronomischen Jahres abweichen. Die endogene Jahresrhythmik ist nicht an vollständige Pflanzen gebunden, sondern ebenso wie auch die endogene Tagesrhythmik noch an Gewebekulturen nachweisbar. Selbst in trockenen Samen besteht die Rhythmik noch, sie hängt also nicht einfach mit einem Wechselspiel biochemischer Vorgänge zusammen.

Discussion

C. A. REINDERS-GOUWENTAK: Der Vortragende erwähnte die Ruhe des Baumes. Vielleicht hat auch die Samenruhe etwas zu tun mit irgend einem Verhältnis Wuchsstoff/Hemmstoff.

F. RESENDE: Nach meinen Untersuchungen (1949–50) ist die jährliche Eigenrhythmik ein wichtiger das Blühen regelnder Faktor und zwar deshalb weil der Quotient Auxin/Antiauxin endonom jahresperiodisch schwankt.

R. HARDER: Das Verhalten von *Kalanchoë Blossfeldiana* in verschiedenen Licht-Dunkel-Rhythmen stimmt nicht immer mit BÜNNINGS Theorie der endogenen Rhythmik überein. Solche Einzelheiten müssen noch geklärt werden. Einstweilen braucht nicht gezweifelt werden an der ausgezeichneten Theorie BÜNNINGS, die als erste eine wirkliche Erklärung der hierher gehörigen Erscheinungen geliefert hat.

H. BORRIS: Wurde in den Versuchen zum Nachweis der rhythmischen Keimungsschwankungen von Samen die Möglichkeit völlig ausgeschlossen, dass diese Schwankungen durch wechselnde Aussenfaktoren induziert wurden? Die Koinzidenz der Keimungskurven von verschieden vorbehandelten Samen legt wegen der bekannten Abhängigkeit der Länge der Ruheperiode von Aussenfaktoren wie Temperatur, Sauerstoff, hier den Gedanken nahe, dass ebenso wie bei den Versuchen anderer Autoren, die ähnliche Schwankungen beobachtet haben, ein übersehener Aussenfaktor geschwankt hat.

A. VEGIS: Die Bezeichnung „endonome Jahresrhythmik“ ist zu vermeiden weil Wachstum und Entwicklung der Pflanzen in hohem Grade von Aussenbedingungen beeinflusst werden, die besonders in den kalttemperierten Zonen nur kurze Zeit optimal sind und zu anderer Jahreszeit die Pflanzen oft Monate lang zu Ruhe zwingen. Dabei sind diese Ruheperioden für die weitere Entwicklung entbehrlich, und wie BLAAUW und Mitarbeiter fanden, kann der normale Zyklus durch Anwendung der jeweils optimalen Temperaturen gekürzt werden (bei *Tulipa* zu 9 Monaten statt 12). Nach den Un-

tersuchungen der letzten 20 Jahre erscheint die Jahresrhythmik der Pflanzen nicht als eine innere Rhythmik, sondern als bedingt durch Schwankungen vor allem der Temperatur und der täglichen Belichtung.

P. CHOUARD (Paris)

Traitements photopériodiques de longue durée; conclusions à en tirer pour la physiologie et l'écologie

L'application de traitements photopériodiques définis, poursuivie *sans interruption* pendant plusieurs années sur plus de 400 espèces, révèle, notamment, le caractère permanent ou temporaire du comportement de la plante au photopériodisme, ses variations avec le vieillissement physiologique, la diversité dans les durées spécifiques de l'induction, et la liaison étroite de ces réactions avec les autres mécanismes régulateurs du développement tels que le thermopériodisme, la dormance et la vernalisation.

De nombreuses conséquences d'ordre *physiologique* peuvent d'abord être tirées de tels essais, soit comme des certitudes expérimentales, soit comme des hypothèses de travail, soit comme un effort de classement logique des faits. Par exemple, on notera une nouvelle classification des types de réactions photopériodiques, plus nombreux et plus complexes que dans les exposés classiques; — la variation de la réaction avec l'âge, avec tendance au caractère « indifférent » avec le vieillissement; — la mise en évidence d'époques d'inexcitabilité photopériodique; — la relation entre « maturité de floraison » et dimensions des meristèmes; — la relation entre la mise à fleurs et l'arrêt ou le ralentissement des phénomènes d'élongation; — les cas de réversibilité et d'irréversibilité de l'induction photopériodique de floraison; — les diverses durées de l'induction; — les nombreux phénomènes de croissance liés au photopériodisme et concernant l'élongation végétative, l'accoutumance des feuilles au photopériodisme dans leurs rôles auxinogènes et

organogènes, les diverses morphoses foliaires et florales; — les processus d'induction autonome ou aïtonomes de la dormance des bourgeons.

Ces considérations éclairent singulièrement l'explication expérimentale des données de l'écologie propre de chaque espèce, et montrent l'extrême importance des facteurs physiques du milieu dans leur allure périodique ou rythmique. De nombreux exemples, tous tirés de l'ensemble expérimental original ici résumé, peuvent être donnés pour montrer comment chaque espèce, par la combinaison qualitative et quantitative des mécanismes régulateurs internes de son développement possède une amplitude écologique définie et, dans chaque station, un comportement phénologique et morphologique défini. De la sorte, une herborisation intelligente devient un préambule à des recherches physiologiques, en même temps que la physiologie éclaire plus complètement l'explication du spectacle de la nature et accroît notre maîtrise sur le rendement des plantes cultivées.

Discussion

G. NOACHOVITCH: M. CHOUARD a compris le grand intérêt que présentent, pour l'étude du photopériodisme, des recherches de physiologie et d'écologie comparées portant sur un nombre considérable d'espèces appartenant à des groupes naturels extrêmement variés. Il a souligné tout à l'heure la nécessité de poursuivre de telles investigations en équipe, le naturaliste coopérant avec le physiologiste. La collaboration du généticien à de tels travaux est non moins indispensable. Car la variabilité intraspécifique à l'égard du photopériodisme est parfois considérable. Un des exemples les plus remarquables de cette variabilité a été récemment mis en évidence dans les cas des riz cultivés à Ceylon, où la différence entre les jours les plus longs et les jours les plus courts est de moins d'une heure. Cette différence est cependant suffisante pour établir une séparation catégorique entre les variétés dont l'épiaison se produit trois mois après le semis quelle que soit la date de celui-ci et les variétés qui ne peuvent

épier qu'après avoir subi l'action des jours les plus longs. Il importe donc d'étudier le comportement par rapport au photopériodisme de génotypes parfaitement définis (tout particulièrement d'homozygotes) sous la forme de lignées pures ou de clones. M. CHOUARD a fait allusion aux modifications de la réaction photopériodique avec l'âge des individus, qu'il a observées dans un certain nombre d'espèces. On peut se demander s'il ne s'agit pas de cas d'inversion de la dominance chez des hétérozygotes résultant du croisement entre des génotypes réagissant différemment à la photopériode.

La variabilité intraspécifique est également souvent très grande quant à l'intensité des réactions morphogènes par rapport aux facteurs externes. Les recherches que poursuivent M. COMBES et ses élèves doivent permettre d'apporter de remarquables précisions non seulement à la systématique linnéenne, mais plus encore à la caractérisation des différents génotypes, en étudiant systématiquement la variabilité phénotypique de leur patrimoine héréditaire. Les agronomes s'attachent à créer des races qui, s'accommodant d'amples variations dans les facteurs du milieu, puissent être cultivées sur des aires étendues. Encore faut-il que de telles races ne manifestent que de faibles variations phénotypiques par rapport aux modifications du milieu. Les méthodes de recherche mis en œuvre par M. COMBES et son école faciliteront beaucoup la poursuite de cet important objectif, ici encore le généticien, le physiologiste, et l'écologiste collaborant étroitement.

R. DE VILMORIN: Je regrette que M. CHOUARD n'ait pas eu le temps d'aborder ici l'importance pratique de ses observations. Elles contiennent pour les agriculteurs et surtout pour les horticulteurs matière à de nombreuses applications: production de plantes fleuries à des dates inusuelles, nouvelles époques de multiplication végétative, nouvelles méthodes de production de graines etc.

R. BOUILLENNE: Je remercie et félicite M. CHOUARD pour son exposé extrêmement riche en informations précieuses. Je voudrais ap-

porter au débat le résultat d'expériences faites à Liège depuis trois ans avec un de nos collaborateurs, C. SIRONVAL, et ainsi répondre à l'appel de M. CHOUARD à la physiologie. *Fragaria vesca* des quatre saisons a été étudié de la graine à la graine. Il présente deux types de faits: 1. Morphologiquement. Il ne fleurit que lorsque la plante a pu former des feuilles de 40 à 50 dents. 2. Physiologiquement. Dans les feuilles de 50 dents, qui ne se forment qu'en jours longs, apparaissent en jours longs dans les cellules de parenchyme en palissade — à côté de cristaux de carotène — des gouttelettes d'huile qui ont été extraites et qui se révèlent

intéressantes comme substances chimiques dans l'initiation de la floraison. L'étude en est présentement entreprise biochimiquement.

Mme REINDERS-GOUWENTAK, incertaine de la valeur du terme nouveau de «nyctopériodique», fait observer qu'il y a une période d'obscurité même en «jours longs».

R. HARDER erörtert die Ausbildung der Blätter bei photoperiodisch reagierenden Pflanzen wenn sie aus einer Tageslänge in eine andere übergesetzt werden.

P. CHOUARD donne quelques explications, entre autre sur l'accoutumance au photopériodisme.

SESSION 7

Jointly with Section FOB: July 18th, 2—5 p. m.

Chairman: DOW V. BAXTER, Recorders: E. BJÖRKMAN and L.-G. ROMELL

SUBJECT:

Forest Sites

S. O. HEIBERG and D. P. WHITE
(Syracuse, N. Y.)

Potassium Deficiency of Reforested Pine and Spruce Stands in Northern New York

Starvation of young coniferous plantations of *Pinus resinosa*, *Pinus strobus*, *Picea abies*, and *Picea glauca* was observed on sandy soils developed on a terrace of glacial outwash in the outskirts of the Adirondack Mountains in New York State. Original vegetation on the area probably included *Pinus strobus*, *Tsuga canadensis*, and *Picea rubens*. This forest was cleared for agricultural crops and grazing during the period 1800–1850. Fairly intensive agricultural use continued until about 1925. The soils are podzolic medium and coarse sands containing 4–5 per cent organic matter in the old plow layer, having a pH of 5.0–5.5 and a medium to low content of available plant nutrients. At the time of reforestation which began in 1928, the principal components of the vegeta-

tion which covered the abandoned fields included *Polytrichum commune*, *Cladonia* sp., *Spiraea* sp., *Andropogon furcatus*. The plantations now exhibit nutrient deficiency symptoms which include: 1. General chlorosis followed by browning and finally dying of needles; 2. Decreased height and diameter growth; 3. Decrease in the number of years that the needles persist on the trees; 4. Shortening of the needles.

Soil mulches of fresh branches from *Pinus strobus* and *Pinus resinosa* as well as *Acer saccharum* resulted in immediate recovery. Applications of mor humus from old *Pinus strobus*-*Tsuga canadensis* stands as well as other applications of complete commercial fertilizer produced a strong growth response, whereas a glass wool mulch gave no growth response. One-tenth acre plots of *Pinus resinosa* treated in May 1943 at pounds per acre rates including 500 pounds CaO, 300 pounds NaNO₃, 100 pounds (NH₄)₂SO₄, 200 pounds Ca₃(PO₄)₂, and 200 pounds KCl resulted in a strong growth

response with only the KCl, and a mild response to the NaNO_3 application. These applications were repeated in May 1946 on other areas, and in addition treatments with 200 pounds per acre of K_2SO_4 , as well as logging slash from fertile sites of *Pinus strobus* and *Pinus resinosa* and poor slash from a *Pinus resinosa* stand were included. The results of these new trials confirmed those previously obtained of a strong response to potassium containing materials. Subsequent fertilization of symptomatically deficient coniferous plantations including *Picea abies* and *Picea glauca* all resulted in a pronounced response to potash fertilization even at the end of one growing season.

Chemical analyses of fall collected needle tissue showed a strong correlation between growth response and a high content of K in the tissue as well as an increased amount of exchangeable potassium in the soil. The highest concentration of K in the tissue, 0.80 per cent of oven-dry weight, was found in the current needles of *Picea abies* fertilized four months before collection, as contrasted to a needle content of 0.21 per cent K on the untreated spruce plot. Current needles collected from healthy or fertilized *Pinus resinosa* and *Pinus strobus* in September contained from 0.45–0.74 per cent K. In no cases did pines which showed deficiency symptoms contain more than 0.34 per cent K in the current needle tissue and usually less than 0.30 per cent. Deficient specimens of *Picea glauca* and *Pinus strobus* contained even smaller amounts of K, the current tissue analyzing from 0.13 to 0.25 per cent.

Plots fertilized with KCl were strongly preferred for food by the varying hare, *Lepus americanus americanus*.

No significant increase of N or Na content of the foliage was found in the pines fertilized with either $(\text{NH}_4)_2\text{SO}_4$ or NaNO_3 .

The increase in annual height growth produced by the potash fertilization was from 46 to 104 per cent over the control plots, and the effect of the 1943 potash fertilization still continues in the 1949 growth.

In all samples the K was concentrated in the

last years needles, whereas the Ca content of the needles increased rapidly with age. Over a period of years the K content of the foliage of fertilized *Pinus resinosa* is declining slightly, but the effect of fertilization over control plots is still manifest in growth and K content of tissue even after a period of 16 years.

The paper, read by S. O. HEIBERG, was profusely illustrated with colour slides.

Discussion

Questions on experimental detail were asked by D. V. BAXTER, R. F. DAUBENMIRE, L. LEYTON, E. GORHAM and D. MÜLLER and answered by Professor HEIBERG.

L. LEYTON (Oxford)

The Growth and Mineral Nutrient Relationships of Trees Growing on Calluna Dominated Sites

Attempts in Great Britain to afforest *Calluna* dominated sites with species like Sitka Spruce have in many cases met with little success, particularly where the *Calluna* cover has not been destroyed. Poor growth has been attributed to the very low fertility of such sites, e.g. P deficiencies in the soil, but attention must also be drawn to the influence of the *Calluna* itself which appears to inhibit the growth of spruce to a far greater extent than that of other tree species like pine. This paper seeks to explain this specific inhibition in terms of the rooting habits and mineral nutrient relationships of the species involved. Data are presented from field experiments set out to compare the effects of screening and of graded applications of phosphatic fertilizer on the growth and nutrition of spruce and pine growing on such sites. The results obtained to date suggest that whilst P deficiencies in the soil are contributory towards poor tree growth, the growth of spruce is more intimately connected with its N status. A close relationship exists between

the N nutrition of spruce and *Calluna* but not with pine. This is undoubtedly connected with the rooting habits of the three species concerned.

The nutrient status of *Calluna* growing on different sites has been studied and significant differences have been found between different communities. In view of the relationship between the N status of *Calluna* and the growth of spruce, the possibility of using *Calluna* as an indicator of site fertility deserves attention.

Discussion

H. H. H. HEIBERG: How is the soil profile?

L. LEXTON: Podsolization varies, is marked in places.

H. ROBAK: Yorkshire heaths in general are more podsolized than those of Western Norway.

E. GORHAM asked about rooting habits of Sitka Spruce and C. H. GIMMINGHAM suggested competition for water between this species and *Calluna*.

L. LEXTON: This may be important but nutrient relationships are also involved.

H. ROBAK referred to the generally low level of phosphate contents found, a fact suggesting that existing differences in this factor, as between pure and mixed *Calluna* heath, may not be without importance.

O. SVANBERG explained the behaviour of manganese on the basis of chemical facts.

L.-G. ROMELL welcomed the thorough study taken up at Oxford of the old problem of heather and spruce, so much discussed all since P. E. MÜLLER's days. Dr. LEXTON's general result agrees with other data indicating a shortage of available nitrogen in undisturbed and typical mor.

H. ROBAK (Bergen)

Growth Check in Young Spruce on Heath in Western Norway

On the West-Norwegian heaths the vegetation is dominated by *Calluna*, other ericaceous species, and *Empetrum*. The soil varies considerably. Earlier investigations show that, although

podsolie in nature, it is rarely a typical podsol. As a rule the humus layer has a relatively high mineral content, the leached layer is thin and not very marked, and very often there are but traces of moor- or ironpan. Precipitation is considerable, and the humus layer has a high water content during a large part of the year although in some types of heath it is rather permeable.

On heaths with *Calluna* prevailing, young spruce suffers a growth check lasting from about 10 to 30 years, varying with humus quality. During check, the plants remain short-necked and yellowish and do hardly show above the heather—a picture long known, for instance from heaths in Jutland. As a rule the plants recover sooner or later, rather suddenly, and from then on yield satisfactory growth. They have previously developed a wide, horizontal root system. Under a shelter of *Pinus silvestris* or *P. mugo* representing the first tree generation spruce plants escape check only when the shelter is removed successively so as not to leave openings wide enough to let *Calluna* in again. On clear-felled areas pine stands on old heath, a grass cover is in the course of 4–5 years replaced by *Calluna*, and newly planted spruces go rapidly into check. This is less pronounced near standing pines.

Spruce plants placed in typical "check soil" lose their mycorrhiza. Prof. HAGEM has obtained a rather long-lasting but not very vigorous growth response by heavy liming and working of the soil in plats prepared in the autumn previous to planting. The limed plants have shown a moderate mycorrhizal equipment of a normal type. In recent field tests with so-called flat-root planting, performed by A. BRANTSEK, an addition of 50 g limestone meal to each plant eliminated check for 4–5 years, yet only on the mildest types of *Calluna* humus does this bring the plants beyond the check period. Superphosphate, likewise, gave a distinct response, more pronounced in older, heavily checked plants. Calcium nitrate and trace elements had no appreciable effect. A test started 1931 still shows a considerable improve-

ment from calcium cyanamide added in quantities sufficient for killing the heather.

C. O. TAMM (Stockholm)

Growth and Nutrient Consumption in a Moss Community

The ecology of *Hylocomium proliferum* (L.) Lindb. and of communities composed of this moss in Swedish spruce forests has been investigated.

The morphology of *Hylocomium* makes it possible to determine its total annual production of dry matter within given areas. It has been found to amount to about 1 ton per hectare under favourable conditions.

The nutrient contents of the living *Hylocomium* are absorbed from the surroundings and not translocated from the old dead or dying parts of the plant, at least not to any great extent. This is concluded from a comparison between the nutrient contents of living and dead annual shoots.

The annual nutrient consumption has been calculated for a *Hylocomium* community, yielding 1 ton of dry matter per hectare. It amounts to approximately 10 kg of nitrogen, 1.5 kg of phosphorus and 5 kg of potassium to the hectare. It does not seem very likely that all these nutrients are supplied from the soil, because *Hylocomium* is not able to draw much water from below (STÅLFELT 1939), and has no roots or other organs adapted for absorption of salts from the soil. In fact it can grow well without any connection with the soil, for example on granite rocks and stones.

The growth of *Hylocomium* is related to the tree canopy (TAMM 1950). Within areas heavily shaded by spruces, the production of the *Hylocomium* community is low, probably due to light deficiency. Away from the tree cover the production also decreases. In some cases this may be due to water deficiency or sunshine injuries, but in the area examined the decrease probably has something to do with the nutrient

supply. A known source of nutrients is the litter shed by the trees (ROMELL 1939). Nutrient salts are easily leached out from this litter. Possibly the rainwater dropping from the trees contains some nutrients washed out from the tree crowns.

It has been established that not only living but also dead *Hylocomium* absorbs calcium. The calcium content of the moss increases with its age. This can be explained if the water passing down through the moss carpet contains some calcium; the moss then absorbs calcium ions in exchange for potassium and, probably, hydrogen ions.

It is pointed out that the study of the nutrient supply to the mosses has a bearing upon the nutrient ecology of the forest trees.

The value of further computations of the nutrient consumption of other plant communities is emphasized.

References

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Discussion

The speaker answered a question on experimental conditions, asked by D. MÜLLER.

H. VAN VLOTEN drew attention to work done at the Belgian Forest Experiment Station on water coming down through the crowns and along the limbs and boles of beech and spruce, influencing acidity and aquatic life of small streams in the Ardennes.

U.S. FOREST SERVICE

Richer Range Rewards (Film)

By courtesy of the U. S. Forest Service and the American Embassy in Stockholm, this sound film in colour was shown following an introductory talk by W. A. DAYTON.

SESSION 8

July 19th, 9 a.m. — noon

Chairmen: W. H. PEARSALL and P. W. BRIAN, Recorder: L.-G. ROMELL

SUBJECT:

Antibiotic Factors in Soil and Peat

P. W. BRIAN, P. J. CURTIS and
E. G. JEFFERYS (Welwyn, Herts.)
*Antibiotics Produced by Fungi Isolated
from Acid Heath Soils*

The concept of microbiological antagonism in soil is now generally accepted. One of the best established of such antagonisms is that which has on many occasions been shown to exist between root-parasitic fungi and the saprophytic soil microflora. Most experimental data refer to conditions in agricultural soils of high fertility. The work of BJÖRKMAN and RENNERT-FELT in Sweden and of RISHBETH in England, on the *Fomes annosus* root-rot of pines, has shown that such antagonisms also exist in relatively infertile, acid soils; a similar conclusion could be drawn from the researches of RAYNER and NEILSON-JONES on mycorrhizal problems.

Microbiological antagonism has received various explanations. In many cases competition for nutrients, the saprophytes being more successful in this competition, has been shown to be a major factor. More recently, the fact that many antagonistic saprophytes have been shown to produce antibiotics in laboratory culture has suggested that their antagonistic effects in soil may be associated with this capacity to produce antibiotics.

Investigation of this hypothesis cannot be made in general terms; the biological and physico-chemical conditions in different soils and under different crops differ so considerably that each distinct case must be specifically investigated. The basic information needed in each case is:

a) What are the antagonists commonly pres-

ent in the soil and what is the nature of the antibiotics, if any, which they produce?

b) What is the stability of these antibiotics in the soil concerned?

c) Can these antibiotics be produced in the conditions existing in the soils concerned?

We have commenced an investigation of the saprophytic microflora of acid heath soils, such as are commonly used for afforestation in England, from this point of view; the present paper deals mainly with the first of the questions given above, an answer to which is a prerequisite to answering the other two.

In acid heath soils the numbers of bacteria and actinomyces present are small. The saprophytic fungi probably assume greater importance than other elements of the microflora. The most abundant fungal antagonists which we have found in such soils, together with the antibiotics they produce, are: *Trichoderma viride* (viridin, gliotoxin); *Penicillium nigricans* (griseofulvin); *Penicillium albidum* ("red pigment"); *Penicillium terlikowskii* (gliotoxin); species of the *Penicillium brevicompactum* series (mycophenolic acid); *Penicillium gladioli* (gladiolic acid); an as yet undetermined monoverticillate *Penicillium* sp. ("frequentin"); a species of *Verticillium* (three antibiotics, rubroverticillin, aurantioverticillin and vertin); several fasciculate *Penicillium* spp. (expansin).

Of these, viridin, griseofulvin and "frequentin" are antifungal but not antibacterial; the remainder are toxic both to fungi and to bacteria though the antifungal activity is usually most marked. Their activity varies from very high (viridin, griseofulvin) to low (the *Verticillium* antibiotics). They differ in their

stability in aqueous solution: griseofulvin and expansin are stable over a wide pH range; viridin and "red-pigment" are unstable except in solutions of low pH; the other substances fall between these two extremes.

The stability of these antibiotics in soil is discussed in another communication to this Congress by E. G. JEFFERYS. It suffices here to say that in an acid heath soil many of these substances show a high degree of stability (e.g. griseofulvin, expansin) and even the least stable (e.g. viridin) are not decomposed so rapidly as to be without biological significance. In a neutral, fertile, loam soil all are much more rapidly decomposed, in some cases as a result of unfavourable pH or, in other cases, as a result of microbiological activity.

We have, at this stage, no conclusive evidence whether these antibiotics can be produced under soil conditions but we consider that the intrinsic physical and chemical properties of at least some of them are such that, if produced, they would persist long enough to exert definite antagonistic effects.

The paper was read by P. W. BRIAN.

Discussion

S. A. WAKSMAN: It may be of interest to add that the bacteria and actinomycetes which are very abundant in less acid and fertile soils also produce a large number of antifungal agents. The actinomycetes are known to produce at least two compounds, actidione and fradecin, which may actually find application in the treatment of fungus diseases of plants.

I would also like to call attention to the nomenclature of patulin. At least three other names have preceded the designation of this antibiotic, certainly one of the most common antifungal agents produced by fungi, namely clavacin, claviformin and expansin. Prof. FLOREY and Prof. CHAIN in their latest monograph are inclined to give priority to the last term.

P. W. BRIAN pleaded guilty in the nomenclatural case and answered a question asked by the Chairman.

ERNA GROSSBARD (London)

The Production of Antibiotic Substances in the Soil

The soil is the natural habitat of many micro-organisms which in laboratory culture produce antibiotic substances inhibitive to the growth of phytopathogens. For an understanding of the mechanism of the biological control of soil-borne plant diseases it appeared necessary to investigate whether the formation in the soil of one antibiotic, or perhaps several, could possibly be induced.

Soils, either completely or partially sterilised and containing straw or glucose or sugar beet pulp, were inoculated with one of 5 fungi known to produce antibiotics on synthetic media. These organisms were: *Penicillium patulum*, two unidentified species of *Penicillium* isolated from the soil, *Aspergillus clavatus* and *A. terreus*. It was demonstrated by biological methods that after incubation of these inoculated mixtures, their centrifugates displayed antibiotic activity against several test organisms, including the phytopathogens *Phytophthora parasitica* and *Bacterium carotovorum*. In the absence of the additional source of carbohydrate no inhibitive agent could be detected in the centrifugates. The addition of as little as 0.3 per cent of glucose induced antibiotic formation, which suggested that available carbohydrate might be a limiting factor, at least in the case of the organisms tested. Otherwise, the soil under investigation contained all other nutrients required for antibiotic production.

The microbial competition operating in partially sterilised soil did not seem to interfere greatly with antibiotic formation, except in one case. However, activity was lower in such soils. It was further shown that the antibiotic substance formed in sterile soil retained its activity for some time even when this soil was exposed to re-contamination, either from the air or by mixing non-sterile soil with it. The degree of activity and the period of persistence varied according to the source of re-contamination, suggesting that the composi-

tion of the re-invading micro-flora had a decisive influence.

Although great caution should be employed in drawing an analogy between results obtained with sterilised soil and those to be expected in the field, it is tentatively suggested that the manuring even of non-sterile soil with sources of carbohydrate may lead not only to a change of the micro-flora but also to the formation of toxins of microbial origin. These antibiotics might act on certain pathogens. That the addition of glucose to non-sterile soil may give rise to antibiotic activity in the soil solution was conclusively demonstrated by JACOBS & NANDI using a modification of the displacement method. Furthermore several workers reported that certain root diseases were suppressed by the addition to the soil of organic materials rich in carbohydrate but poor in nitrogen. The depressing effect on the antibiotic titre due to the addition of nitrogenous fertilisers to wheat straw cultures of *P. patulum* was shown by the author. It appears, therefore, that at least in the case of the tested organisms there is a similarity in requirements for antibiotic formation in the soil in vitro and the treatments which bring about the control of certain root diseases.

The mechanism of microbial antagonism is very complex and it is unlikely that a single factor, such as carbohydrate decomposition, will always be the important regulating one. Using different antagonists a different manurial programme will be essential. JACOBS & SINHA have shown that under certain conditions the addition of dried blood to non-sterile soil may give rise to antibiotic activity in the soil solution. Nevertheless, we cannot entirely dissociate the observations made on the control of certain root diseases by carbohydrate manuring from the possibility that this treatment might have led to the formation and action, though perhaps only temporarily, of antibiotic substances, in view of the experimental data provided by JACOBS & NANDI and by the author.

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D. PRAMER and R. L. STARKEY
(New Brunswick, N. J.)

Streptomycin in Soil

Due to its chemically basic characteristics, streptomycin is adsorbed by soil materials and is not readily extracted. Water extraction of soil containing 1000 micrograms per gram released from 0-20 per cent; up to 40 per cent was recovered by extraction with acid alcohol. It appeared unlikely that extracts could be used for the quantitative determination of streptomycin in soils. A method based on a different principle was devised whereby it was possible to determine streptomycin quantitatively in soil containing 10 micrograms or more per gram of soil material. Smaller amounts could be determined by a modified procedure. Streptomycin added to clay minerals (glauconite, kaolinite, bentonite) at reactions of pH 5.0, 6.5 and 8.5 was quantitatively determined even though practically all of the streptomycin was adsorbed. Streptomycin added to clay fractions of various soils at reactions from pH 4.5 to 8.5 could likewise be quantitatively determined. Streptomycin was also quantitatively recovered from complete soils that contained both inorganic and organic colloidal material. The soils varied in reaction from pH 4.6 to 7.5. There was no evidence of disappearance of streptomycin that was added to sterile soil during an experimental period of three weeks. The material disappeared from normal soil and this is ascribed to decomposition by micro-organisms. There was an initial lag of 2 to 7 days after which decomposition was rapid and complete by 14 days. In soils that received additions of readily decomposable organic matter

decomposition of streptomycin was somewhat slower than in untreated soil. The second and third additions of streptomycin disappeared more rapidly than the first addition.

The paper was read by S. A. WAKSMAN.

Discussion

Miss GROSSBARD referred to studies made at the Imperial College in London by S. E. JACOBS and P. SINHA, who observed very remarkable changes in the composition of the microflora when garden soil was treated with streptomycin. There was an initial depression of bacteria and actinomycetes followed by rapid multiplication, maximum numbers being reached when the streptomycin had almost disappeared. This was particularly marked with the nitrifying and cellulose decomposing bacteria and suggests that certain organisms might utilise streptomycin as a food. The same workers have obtained evidence to suggest that the adsorption of streptomycin was a base exchange phenomenon.

J. L. RAMAUT (Liège)

*Recherche sur le rôle de *Sphagnum recurvum* dans l'acidité des tourbières de la Baraque Michel*

Baraque Michel est une région de la Haute Belgique (altitude 675 m) caractérisée par la présence de nombreuses tourbières.

L'acidification de l'eau météorique au contact du *Sphagnum* vivant ou mort et même de la tourbe a fait depuis longtemps l'objet de nombreuses observations.

Divers auteurs tels BAUMANN et GULLY, SKENE, BEYERINCK, BAAS-BEKKING et NICOLAÏ, BOUILLENNE et L. DELARGE ont mis cette propriété en évidence d'une manière tout à fait indiscutable et en ont même mesuré l'intensité.

En général, ces études n'ont pas dépassé le stade de l'observation, on s'est limité à la simple constatation d'une diminution de la valeur de

pH de l'eau de pluie ou de tourbières voire de certaines solutions salines au contact du *Sphagnum* ou de la tourbe.

L'étude expérimentale de l'acidification a toutefois été abordée par quelques chercheurs tels BAUMANN et GULLY, PAUL et BAAS-BEKKING.

Les résultats obtenus et surtout leurs interprétations manifestent de très grandes divergences.

N'ayant aucune base certaine, nous avons repris dans son entièreté le problème de l'acidification de milieux naturels ou synthétiques par le *Sphagnum*.

A. Nos expériences nous ont conduit à examiner les variations de pH de milieux naturels (eau de tourbières, eau du Puits du Mont-Rigi) au contact de *Sphagnum recurvum* vivant et ce, dans des conditions expérimentales nettement définies. Ces mêmes expériences ont été réalisées dans les mêmes conditions avec des milieux de culture synthétiques. Elles nous ont permis de conclure que:

1. Le *Sphagnum recurvum* vivant acidifie avec des intensités variables les divers milieux que nous avons utilisés. L'intensité du phénomène est liée à la nature du milieu et à son pH initial.
2. On observe toujours après un certain temps de culture une stabilisation du pH du milieu.
3. Une nouvelle phase d'acidification s'obtient si l'on renouvelle le milieu de culture.

B. Dans une nouvelle série d'expériences réalisées avec les mêmes milieux mais dans des conditions expérimentales différentes (obscurité, atmosphère d'azote), nous avons pu déterminer que:

1. A l'obscurité, l'intensité du phénomène est plus grande qu'à la lumière. Les facteurs photosynthétiques ne paraissent pas associés au phénomène.
2. En atmosphère d'azote, il n'y a pas de différences comparativement à l'atmosphère normale. Ceci porterait à penser

que le phénomène n'est pas sous la dépendance du métabolisme oxydatif.

- C. L'examen des réactions du *Sphagnum recurvum* tué en chaleur sèche a montré que ce dernier acidifie également les divers milieux utilisés mais avec une intensité plus faible que les brins vivants.

Toutes ces observations nous ont amené à envisager dans le phénomène d'acidification, le passage d'un ou plusieurs éléments acides des cellules du *Sphagnum* dans le milieu extérieur.

- D. Nous avons alors tenté l'isolement de ce corps responsable et par diverses modalités d'extraction, nous sommes arrivés à préciser que:

1. L'action de l'alcool éthylique et l'éther sulfurique sur le matériel desséché donne lieu à une extraction d'une fraction du pouvoir acidifiant.
2. Des extractions successives par une gamme de solvants dans un ordre déterminé permettent d'extraire la totalité du pouvoir acidifiant. On dispose à ce moment d'un extrait brut contenant les composés responsables.

En absence de M. RAMAUT, la lecture a été faite par M. R. BOUILLENNE.

Discussion

S. VILLERET: La présence de l'acide carbonique (et par suite de CO_2) dans les eaux très faiblement minéralisées des tourbières est aussi responsable de l'acidité actuelle de ces eaux. Les dosages de CO_2 effectués par nous dans ces eaux ont toujours révélé une concentration de CO_2 suffisante pour amener à un pH d'environ 4 des solutions minérales aussi peu tamponnées

que les eaux de tourbières. La disparition expérimentale du CO_2 dans l'eau des tourbières s'accompagne de l'élévation du pH vers la neutralité, tandis que la recharge artificielle de cette eau s'accompagne d'un abaissement du pH jusqu'à 4,0 et même 3,8.

D. A. WEBB could not attribute a predominant role to CO_2 in very acid waters because it is impossible to realize a sufficiently low pH by any concentration of CO_2 that can remain in contact with air. He asked whether the acid can be concentrated from aqueous solutions; whether the titer of water placed in contact with living *Sphagnum* reaches a constant value (as well as the pH); and whether there is any information available on the stability of the acid in aqueous solution. This last question was asked because in the west of Ireland are many lakes, lying in silicious basins, surrounded by bogs with water of pH 4.2, but themselves containing almost neutral water. Their neutrality is due not to added base, but to disappearance of acid from the bog water, apparently by oxidation or precipitation.

L. PLANTEFOL a pu montrer que les membranes des Mousses — et des Sphaignes en particulier — ont la propriété de réaliser extrêmement rapidement, en présence de l'oxygène de l'air, l'oxydation de nombreuses substances organiques, en particulier des acides. Un lien physicochimique peut donc sans doute être trouvé entre l'acidification des eaux par le CO_2 , à laquelle on vient de faire allusion, et la production d'une matière acide séparable par extraction. Il est possible que la Sphaigne élabore un acide qui diffuse au travers des membranes, et que celui-ci, au cours de ce passage, subisse la dégradation qui expliquerait pour une part la présence de CO_2 dans l'eau de la tourbière.

SESSION 9

July 19th, 1—4 p. m.,

Chairman: W. H. PEARSALL, Recorder: L.-G. ROMELL

SUBJECT:

Soils

W. H. PEARSALL (London) *Ecology of Wet Soils in Britain*

High soil humidity functions mainly through its effects on soil aeration. The effective limits of aeration are not easily defined by any method of gas analysis. They can be recognised either by measurement of oxidation-reduction potentials or by the nature of the biological decompositions going on in the soil.

Above a potential of 0.3 and 0.35 V at pH 5 the soil reactions are predominantly oxidising e.g. nitrates are produced rather than ammonia. Below this level products like sulphides, methane and ferrous ions accumulate. In lake muds at pH 7, the potential boundaries at which these changes take place lie as follows:

nitrate—nitrite	0.45—0.40 V
nitrite—ammonia	0.40—0.35 V
ferric complex—ferrous complex	0.3 —0.2 V

The oxygen concentrations associated with these potential ranges were approximately 4, 0.4 and 0.1 mg per litre respectively.

A few soils such as highly organic lake muds and very wet bog peats may be permanently reducing but in most soils there is a phase of oxidation in summer at least and this increases in duration and intensity as the soil becomes drier.

A characteristic feature of reducing zones is that mineral ions are more readily available. Thus in the soil of a *Molinia-Lythrum* area (Blelham Tarn) the following differences were observed during the oxidising period in summer and the reducing period in winter.

Exchangeable cations in a swamp soil

	pH	Ca	Mg	Fe	Mn	Al
July	5.53	242	27	3	0	4
January	5.67	279	59	248	19	8

Wet soils in Britain are almost always peaty and the humidity of such soils is most conveniently measured as the Relative Humidity of CRUMP, i.e. water content/humus content. The usual summer value of this ratio in northern Britain for such vegetation types as heather moor and oakwood is from 2 to 3. Wet woodlands commonly have values below 7 in summer and soils with values of 12 or more in summer are generally reducing soils, oxygen entering only by diffusion from the surface. The difficulty about using this ratio is that the samples have to be collected under comparable conditions and it is therefore difficult to get a wide series of comparable results. However, examples will be given in illustration.

The pH of most wet soils tends to vary not only with the degree of base-saturation but also with the degree of oxidation. Permanently reducing soils like lake muds are normally not very acid, thus MISRA found that out of 94 non-calcareous lake muds examined, none was below pH 5.3. They ranged upward to pH 7.4. In the very wet Connemara bogs bearing vegetation of *Sphagnum*, *Molinia*, *Erica*, *Calluna* with *Schoenus* or *Rhynchospora* and in a rainfall of 230–250 cm per annum, the pH ranged from 4.66 to 5.46. The pH diminishes from these figures as the duration and intensity of oxidation increases. Thus on following a succession

of vegetation we may get a decreasing pH as the water content diminishes and oxygen content increases.

When peaty soil is drained or burned, oxidation follows and the acidity increases in the same way.

If the pH range of the surface of raised bogs is determined in areas with varied rainfall, there is a general correlation between increased acidity and lower rainfall.

Finally the character of the soil organic matter shows some relation to these variations of humidity and acidity. The distinction between the types of humus called *Mull* and *Mor* is well known but it is perhaps not so clearly recognised that even in wet soils the character of the processes of decay shows similar differences at the alkaline and acid ends of the soil series. Even in very wet reed-swamp soils the processes of decay are such that carbon is lost more rapidly than nitrogen, provided the humus is partly base-saturated. In base-deficient soils however, whether wet or dry, the proportion of nitrogen diminishes so that the carbon-nitrogen ratio always tends to be relatively high. The influence of water-logging on these processes of decomposition seems to be much less than is usually thought and the influence of base deficiency is evidently very important.

Discussion

Explanations were given as follows by the speaker in reply to questions asked by G. DELOFFRE, D. MÜLLER, and L.-G. ROMÉLL. The exchangeable hydrogen in the soils described changes in a roughly inverse proportion to the exchangeable base. In the oxidising phase of a wet soil, the exchangeable hydrogen is rather higher than in the reducing phase. The lower pH of better aerated soils seems to be due not to the formation of nitrate or sulphate but to structural changes in the soil humus. The acidity of the soil humus seems to be higher in base-deficient soils in Britain in contrast to what SANTE MATTSON found. The statement is based on estimates of the dissociation constant

in the different cases and there is a possibility of a difference of result owing to the different methods used.

G. LOHAMMAR: Following drainage of wet soils in Northern and Central Sweden, high soil acidities occur that are due to the oxidation of sulphides to sulphates. With soils poor in bases there is free sulphuric acid in the soil solution.

V. J. CHAPMAN and J. W. RONALDSON
(Auckland)

Mangrove Soils in New Zealand

A detailed study is in the process of being carried out on the mangrove and salt marsh soils of the Auckland isthmus. The soils fall into several different types depending on the relative proportions of sand and mud. The basic structure of swamps is of three categories:

- a) soft mud throughout
- b) mud overlying fresh water peat
- c) sand overlying mud

There are definite seasonal variations in the chemical constituents of the soil, and the soft mangrove mud appears to differ from the other groups. Movement of the water table is most pronounced in the sub-peat layer when present. The upper layers do not become water logged when the swamp is flooded by the tide.

The swamps and marshes form behind mobile shell bars, which develop in different places. Rates of accretion have been measured and a tentative time scale established.

The paper was read by V. J. CHAPMAN.

Discussion

W. H. PEARSALL: It was pointed out that the presence of sand or of an oxidising layer in a clayey maritime soil often results in a difference in vegetation. Did the mangroves on the two different soils, one with an oxidising layer of peat, show any difference in growth?

V. J. CHAPMAN: No, there was no difference.

G. DELOFFRE (Lille)

L'inondation à l'eau de mer de la région de Dunkerque en 1944—1945, ses conséquences sur les sols et sur le développement de la végétation

Après l'inondation à l'eau de mer, en 1944—1945, de 18 000 hectares de terres de la Flandre maritime française, nous avons observé successivement:

1. Une phase d'élimination des chlorures,
2. une phase de dégradation de la structure des sols.

Le lessivage des chlorures entraînés par les eaux d'infiltration a été assez rapide et, en général, suffisant après un hiver. Sauf les Pois, les Haricots, les Fèves, les Lins, la plupart des récoltes n'ont pas présenté d'arrêt de croissance en relation avec un accroissement de la concentration saline de la solution du sol, au cours des périodes sèches en 1946. Nous n'avons d'ailleurs jamais observé d'espèces strictement halophiles comme *Salicornia*, *Salsola*, etc. Les espèces qui se sont installées et ont dominé après l'inondation ont été *Ranunculus sceleratus*, puis *Atriplex hastata*, *Chenopodium rubrum*, espèces plutôt nitrophiles.

La dégradation de la structure de ces sols devenus sodiques est apparue, au cours de l'hiver 1945—1946, après un certain temps de latence elle s'est ensuite développée, surtout dans les sols argileux, au cours des hivers de 1946 à 1950. Ces sols dégradés sont boueux, imperméables, peu aérés par temps humide, et très durs par temps sec. Nous y avons observé depuis 1946 une germination tardive et irrégulière souvent échelonnée en plusieurs poussées successives en relation avec les chutes de pluie. Les jeunes tiges ont une forme tortueuse. Pour les céréales le tallage est plus tardif et moins abondant.

Agropyrum repens et *Phragmites communis* se sont développés davantage dans ces sols que dans les sols non inondés.

Des épandages de sulfate de chaux ont permis de prévenir la dégradation de la structure ou d'y remédier.

Dans les parties basses et dans les fossés qui étaient à l'abri de l'air pendant l'inondation, nous avons observé une réduction bactérienne des composés soufrés et une formation de sulfures de fer qui ont coloré en noir les couches superficielles du sol et la vase des fossés. Après l'inondation l'oxydation de ces sulfures et leur réaction sur le calcaire ont abouti à la formation sur place de sulfate de chaux.

Nous n'avons observé aucune dégradation de structure et les récoltes se sont développées normalement dans ces parties basses et aux emplacements où la vase de curage des fossés a été épandue.

E. GORHAM (London)

Soil Status and Nutrient Uptake by Natural Vegetation

A study has been made of some plant-soil relations in a wooded hillside *catena* along the shore of Windermere, in the English Lake District. From the original glacial clay loams, topography has determined the development of brown earths with *mull* humus on the flushed soils along the lake shore; while podzolic types with surface *mor* humus accumulations are found on the heavily leached hillside.

On the brown earth is an ash-sycamore-hazel tree community, with an open and predominantly herbaceous ground cover. On the leached areas the dominant oak is accompanied by birch and rowan, with a ground flora chiefly of grasses and mosses.

Uptake of minerals and bases has been measured by determining the ash content of the plants and the *excess base* of the ash. The groups and species typical of the flushed sites generally accumulate more mineral matter and more *excess base* than those dominating the leached series.

Nitrogen is higher in herbs, which characterize the brown earths, than in the grasses and mosses, groups more abundant on the leached soils.

Iron assimilation by plants is similar on both soil series. Manganese is slightly less than iron in plants from flushed habitats, and markedly

exceeds iron in those on leached sites. Mosses tend to absorb iron selectively, while woody plants usually concentrate manganese.

SESSION 10

July 20th, 9 a.m. — noon

Chairman: D. I. ARNON, Recorder: L.-G. ROMELL

SUBJECT:

Relations to Nutrients

W. R. C. ATKINS (Plymouth)

Chemical Evidence on the Abundance and Botanical Composition of the Marine Phytoplankton

The water 20 miles from shore off Plymouth is representative of a large area subjected to uniform meteorological conditions and not normally affected by water movements from areas under other conditions. Accordingly the chemical changes between the winter and early summer may be accepted as indications of phytoplankton activity; calculated for a depth of 70 m the changes in carbon dioxide and in phosphate gave as a minimum the production of 1400 metric tons wet weight per square kilometre, whereas changes in silicate indicated only 110 tons. HARVEY's figures for nitrate gave results close to those for phosphate and carbon dioxide. The discrepancy may be due to growth of flagellates and nonmotile green cells without siliceous walls, and too small to be retained by the finest silk nets. The diatom tests do not dissolve or do so very slowly. Very fine clay particles in this area may amount to about one part in a million, and silicate goes into solution from this quite perceptibly in three months, as shown by storage in polythene bottles. This additional source of silicate reduces the discrepancy, but it is improbable that it closes the gap.

Productivity may be followed also by chlorophyll estimations, after filtration through colodion or fine paper, after addition of potassium

aluminium sulphate which gives a gelatinous precipitate in which small flagellates can be seen under the microscope. Extraction with acetone yields yellowish green solutions in which chlorophyll can be determined against a standard using a Schott RG1 filter which transmits red light only. Production was followed thus during 1948 and 1949. The maximum yield was 4.3 mg chlorophyll per cubic metre; the outbursts were in spring or summer, with lesser ones in autumn. The yearly minimum was in August. Dr. M. PARKE's pure cultures afforded counts per milligram of chlorophyll, which, excluding large diatoms, ran from 50 to over 3000 million cells. Thus with 4.3 mg chlorophyll per cubic metre only the very smallest species would show one cell per haemocytometer field as against 350 000 for red blood corpuscles. In addition to distinction by means of silica it is probably possible to estimate the proportions of some of the constituents of the phytoplankton by means of their carotenoids and to this end extracts have been made from pure cultures.

The paper was read by Dr. MARY PARKE because Dr. ATKINS had had to leave before the meeting.

Discussion

Technical questions were asked by T. BRAARUD, D. J. D. NICHOLAS, and G. HYGEN. Replies were given by Dr. PARKE.

In reply to a question by E. C. WASSINK on relative production of land and sea, W. H. PEARSALE pointed out that the mouth of the English Channel has oceanic water with a lower productivity than would be obtained in wholly coastal waters or enclosed seas like the North Sea.

J. W. G. LUND (Ambleside)

Chemical and Habitat Factors in Relation to Freshwater Phytoplankton

Recent researches carried out at the laboratory of the English Freshwater Biological Association are discussed in relation to the problem of what factors govern the productivity and periodicity of phytoplankton. Much attention has been paid to the diatom *Asterionella formosa* Hass with special reference to its occurrence in the English Lake District. The results of the observations and experiments on *Asterionella* together with cellular analyses are pertinent to phytoplankton problems as a whole. In addition the total phytoplankton production of the main lakes in the district has been assessed in relation to the available supplies of carbon, silicon, nitrogen, phosphorus, calcium and iron. Provided certain physical, chemical and biological factors are assessed quantitatively, it is possible to explain and forecast the changes in the size of the populations of *Asterionella* in certain lakes. The view is held that we are not yet in a position to understand why oligotrophic lakes are so much poorer in phytoplankton than eutrophic ones, apart from the well-known fact that lakes lying in drainage basins with fertile soils usually produce large, while those in infertile basins produce small crops of phytoplankton.

Discussion

T. BRAARUD commented on two points which he had found particularly interesting: the demonstration given of parasitism as an ecological factor in phytoplankton, and the effect of silica concentration on density of diatom population. Some marine diatoms appear extremely adapt-

able with respect to silica requirements, as seen in experiments on *Skeletonema costatum* and from the survey made of the Oslofjord. Experiments correlating the actual rate of multiplication with concentration of silica seem most desirable.

Replying to questions asked by Dr. RUTH PATRICK and Dr. MAUD GODWARD, Dr. LUND explained that no investigations had been made on vitamins and that he had no idea as to which of the many substances in the bottom deposits is the one permitting the growth of *Asterionella*; it is not even clear as yet, whether it is inorganic or organic.

D. I. ARNON (Berkeley, Calif.)

Inorganic Micronutrient Requirements of Higher Plants

In the last thirty years it has become abundantly clear that the "classical list" of ten inorganic elements essential for plant growth should be supplemented by several other elements, sometimes designated micronutrients, which are required by plants in minute quantity. In 1937 when our laboratory embarked on the study of micronutrient requirements of plants it was known that boron, manganese, zinc and copper were important in the physiology of higher plants and were involved in a number of soil-plant problems of agricultural importance, but there was no unanimity of opinion as to the essentiality of all of these four elements for plant growth. Our approach to the problem was first to formulate definite criteria of essentiality to test the status of a given element and, second, to apply refined and, whenever possible, quantitative procedures for the purification of the nutrient medium to free it from contamination by the element under investigation.

The criteria established were that an element is not considered essential unless a) a deficiency of it makes it impossible for the plant to complete the vegetative or reproductive stage of its life cycle; b) such deficiency is specific to the

element in question, and can be prevented or corrected only by supplying this element; and c) the element is directly involved in the nutrition of the plant quite apart from its possible effects in soil or other culture medium. From that standpoint a favorable response from adding a given element to the culture medium does not constitute conclusive evidence of its indispensability in plant nutrition.

The experimental procedure used was applicable primarily to metals. It involved the use of the water culture technique with pyrex glass containers, glass distilled water containing less than 0.0002 mg per liter and purified salts containing less than 0.0001 mg per liter of metals as an impurity. This technique has demonstrated with consistency the essentiality, according to the above criteria, of manganese, zinc, and copper in the nutrition of higher plants. Furthermore, evidence was obtained and was since confirmed in other laboratories, in favor of including a new essential element, molybdenum, in the list of micronutrients. Our experience has also led us to some general conclusions about the likelihood of the present list of five micronutrients, boron, manganese, copper, zinc and molybdenum proving incomplete and requiring the addition of other micronutrients yet to be discovered.

Reference

- ARNON, D. I. Growth and Function as Criteria in Determining the Essential Nature of Inorganic Nutrients. University of Wisconsin Centennial Symposium on Mineral Nutrition of Plants. University of Wisconsin Press, 1949.

Discussion

Answering a question by D. J. D. NICHOLAS on cobalt, Dr. ARNON said this is one of the most fascinating elements at the present time.

L.-G. ROMELL drew attention to the old problem of "appétence géique" (SAINT-LAGER) and its possible relation to micronutrient requirements or tolerances.

D. MULDER touched the same question asking why some *Viola* species should have specialized on soil with an excess of zinc.

A. ÅSLANDER (Stockholm)

Lime and Agricultural Plants.

A Discussion of the Problem in Its Bearing on Plant Ecology

Investigations during the past twenty years have revealed that even the most exacting crop plants, for instance barley and sugar beets, grow splendidly in acid media and in "lime-deficient" soils when the supply of nutrients is adequate.

In suitable culture solutions at pH 4.0 barley grew as well as in a neutral solution. Soil analyses have shown that neutral soils in arid parts of the country are comparatively rich in easily available plant nutrients. This explains their fertility. Acid soils found within humid regions are podzolized, poor in plant nutrients, and only after a suitable addition of nutrients can they support exacting crops. No arable soils really deficient in calcium have been found while phosphorus-deficient soils are very common. The calcium content generally exceeds the phosphate content hundred times or more. When acid soils in pot cultures were (by additions of plant nutrients) made as rich as neutral soils (without change in soil reaction), barley grew as well at pH 5.0 in mineral soils and at pH 4.0 in peat soils as at pH 8.0 in mineral soils. On arable land, mineral soils more acid than pH 5.0 or peat soils more acid than pH 4.0 have not been found. The absorption of nutrients, for instance of P, by plants was unaffected by soil reaction. Nodules were formed profusely on red clover in a soil at pH 4.5 when the availability of phosphates was increased by suitable fertilization.

On fields properly fertilized, liming up to neutrality failed to increase the yields sufficiently to make liming profitable. The chemical composition of the plants and their feeding value were scarcely influenced by liming.

On the basis of the accumulated experience a scheme of proper fertilization has been drawn up. According to this scheme, fertilization is in every case calculated on the basis of soil analyses and the requirements of the crops to

be grown. In order to prevent phosphorus fixation in acid soils, phosphates are given mixed with farmyard manure or other humus-forming material.

The difference between fields that are, in the opinion of the farmers, suitable and those that are not suitable for sugar beets has been found to be a difference in plant nutrients and not in pH-value.

Sheep sorrel, *Rumex acetosella*, commonly claimed to indicate lime deficiency, has been found to grow both in nature and in pot cultures as well on slightly alkaline as on acid soils. The limiting factor for distribution of this species is the light conditions of the habitat. The seedlings grow very slowly. Only in a sparse vegetation are they able to survive. Other weeds claimed to indicate a neutral soil reaction or soils rich in lime have been found to grow on acid soils recently fertilized. They were supplanted later on, when crops had depleted the soils, by weeds claimed to indicate lime deficiency or an acid soil reaction.

Analyses of some soil samples collected in various plant habitats on Kinnekulle show that spruce, *Picea excelsa*, dominates where the soil has a low content of easily available phosphorus, and birch, *Betula alba*, on soil with a somewhat higher phosphorus content, while oak, *Quercus petraea*, ash, *Fraxinus excelsior*, linden, *Tilia cordata*, cherry, *Prunus* sp., and beech, *Fagus sylvatica*, seemed to thrive only on soils comparatively rich in phosphorus.

It is concluded that amounts of easily avail-

able plant nutrients, often phosphorus, play a greater part than lime content or soil reaction in determining crop yields and plant distribution.

Discussion

W. A. ALBRECHT had found Dr. ÅSLANDER's paper a very good presentation to show facts in the field supported by fundamental scientific information, and good practices known by farmers. He asked a few technical questions and referred, in concluding, to the need of remembering salesmen's propaganda and of bringing the facts of plant science and of soil science into clearer focus.

W. H. PEARSALL: In regard to direct effect of pH, it is generally the rule that plant proteins are precipitated below pH 4, which is thus usually a lower limit to root growth. A few plants, *Calluna* and others growing on acid soils, have a protective mechanism which prevents this injury effect.

D. I. D. NICHOLAS: In the acidity complex it has been shown that the following deficiencies may occur in susceptible crops: Ca, Na, P, N, Mg, Mo. In addition, the micronutrient elements Mn and Al may exert toxic effects.

A. ÅSLANDER answered technical questions and gave reasons why Swedish soils need little liming. They are young, and lime is added to them by commercial fertilizers and farmyard manure in greater quantities than those taken up by crops.

EXPERIMENTAL TAXONOMY, EXT

President: T. H. GOODSPEED

Vice-Presidents: TYGE W. BÜCHER, J. W. GREGOR, DAVID D. KECK, IRENE MANTON,
G. MELCHERS, OLAVI MEURMAN, E. R. SEARS, MARIA SKALINSKA

Recorder: G. TURESSON

Vice-Recorder: HEDDA NORDENSKIÖLD

SESSION 1

July 12th, 2—3 p. m.

Chairman: G. TURESSON

SUBJECT:

Introductory Meeting

T. H. GOODSPEED (Berkeley, Calif.)

Presidential Address

As you know, important advances in one subdivision of biology have, historically, awaited the stimulation of new evidence or ideas contributed by allied fields of research or, particularly in physiology, new basic concepts in the physical sciences. To be effective these periodic revitalizations involved, in the first place, proper appreciation of the possible significance for any given discipline of discoveries in another—oftentimes a tardy appreciation because of extreme conservatism or because of lack of the requisite scientific imagination—and, in the second place, required proper judgements in the application of new data in one field of research to methodology and interpretation in another.

Although taxonomy as a synthesizing aspect of botany should be a reflection of comparative data from all other aspects of plant science and although its progress should stem in large part from advances in the latter, there has been in the past some justification for the complaint that taxonomy was not as sensitive as it might have been to new viewpoints or

alterations in emphasis. So far as the last half century, at least, is concerned such criticism is not entirely valid. As a student I remember the impact of what was then referred to as the "New Botany," sponsored many years ago by COULTER and his colleagues at Chicago, in which the significance of ontogeny or life histories for interpretation of relationships was more broadly applied than before. Certainly within the past few decades taxonomy has begun actively to appropriate pertinent evidence from allied fields almost as rapidly as their basic concepts and methodologies have evolved. As a result, taxonomy today possesses a considerable series of subtitles—such as cytotaxonomy, phylogenetic taxonomy, biosystematics and experimental taxonomy—some of them essentially synonymous, all to some extent overlapping in content, most of them representing variously weighed emphases and each one directed toward the perfection of a classification picturing, in so far as possible, the actual evolutionary development and the current relationships of the organisms in question, which is of course the unalterable objective of all taxonomy.

The current subtitles under taxonomy just

referred to may be roughly classified under two headings: those that are primarily "experimental" and those that are primarily observational, no sharp line of demarcation being possible. Under the first heading, "experimental," numerous actual tests have been carried out to determine intra- and especially interspecific compatability, meiotic chromosome behavior particularly in F_1 interspecific hybrids, the effects of transplantation to varied environments or substrates, serum reactions and the like. Such investigations are experimental *means* to a taxonomic *end* and not ends in themselves taxonomically—judgement of relationship which is the core of taxonomy is obviously not subject to experiment however much weight it may be required to give to the findings of the experimental approaches. Since the essence of taxonomy does not rest upon an experimental foundation it has seemed to some that the title of this Section, "Experimental Taxonomy," is something of a misnomer and the Section may wish to give some consideration to the proposing of an alternative title to be used in the future. In addition to the so-called experimental contributions to taxonomy there are the largely observational ones—morphological, anatomical, cytological, phytogeographical and paleobotanical.

As I have said, this classification of taxonomic subtitles into "experimental" and "observational" cannot be made mutually exclusive, something which becomes obvious if one attempts a broader classification of the elements of what we are calling "Experimental Taxonomy." Such a broader classification might be made on the basis of what can be called major non-taxonomic approaches to taxonomic problems. These major approaches might be designated the *cytogenetic*, the *morphologico-anatomical*, the *ecological*, the *paleontological* and the *comparative biochemical*.

Taking them up, briefly, in that order we come first to the *cytogenetic* approach. The rise of modern genetics with the beginning of the 20th century has obviously had far-reach-

ing implications for taxonomy. At the moment, emphasis upon the genetic structure of populations is casting new light upon the status of taxonomic categories and is pointing to the futility of attempting all-inclusive definitions of species. On the other hand, that degree of interspecific sterility, as revealed by genetic evidence, can be made an absolute or even perhaps primary criterion of relationship is becoming more and more doubtful. Cytology, on a genetic base, has made certain unit contributions to taxonomy, indeed (in some instances at least) chromosome number and chromosome morphology have become specific characters of some diagnostic value as well as aiding in elucidation of certain problems of phylesis. Polyploidy as revealed by chromosome number and its origin and significance by meiotic chromosome behavior in hybrids may, as in the genus *Nicotiana*, provide a background for interpretation of intrageneric relationships and mechanisms of evolution.

Turning now to the *morphologico-anatomical* approach—it has analysed and extended the research in comparative anatomy carried on so successfully by European investigators during the 19th century. The current interpretation by I. W. BAILEY and his associates of combined morphological and anatomical characters should prove to be increasingly fruitful in attempts to analyze interrelationships of larger taxonomic categories above the threshold of ready genetic investigation.

What may be termed the *ecological* approach has been concerned primarily with demonstrating the existence of genetically determined physiological entities. As you know, the work of TURESSON and of CLAUSEN, KECK and HEISEY has shown that members of morphologically similar populations may exhibit differential physiological responses to uniform environments, thus giving rise to the recognition of climatic ecotypes and attributing to them considerable discreteness. It appears that such climatic ecotypes may now be subdivided into a series of edaphic subecotypes. Rapidly increasing knowledge of the vegeta-

tion of botanically unknown or little known areas, gathering of data in statistically significant amount in familiar ones and greater precision in vegetation mapping have greatly augmented the value of phytogeographic and ecological evidence for taxonomic purposes.

The *paleontological* approach involves important new discoveries which bear upon relationships, notably of the Gymnosperms. Statistical analysis of fossil pollens is providing data concerning past climates and migrational histories. Increased attention to anatomical features, made possible by improved techniques, permits more satisfactory determination of fossils and ecological comparison of past with living plant communities has reversed certain former concepts.

The contribution of the *comparative biochemical* approach is largely an anticipatory one. It appears that chemical analyses of plant substances and products, and perhaps serology as well, should yield clues to relationship but this promising field has as yet been relatively little exploited as to its taxonomic significance.

This classification of approaches and contributions to taxonomic problems illustrates the immensely broadened scope of modern systematics, evidence of which is contained in the titles of the papers to be read in this Section and in joint meetings with the Sections which are specifically concerned with the techniques and points of view of certain of the approaches to taxonomy which I have defined. To me the many faceted content of our topic has one primary objective—i.e. to assist in reducing the area of subjective judgment embodied in all taxonomic decisions. To this end we must recognize that taxonomy as an evolutionary synthesizer can make use only of comparative data, that in arriving at conclusions concerning relationships and classification it must be permitted to make a balanced evaluation of the data we submit to it and, finally, that taxonomy is under the necessity of making practical decisions, something that may in many instances preclude the employment in detail of such approaches as, for example, cytogenetics or geneecology.

SESSION 2

Jointly with Section GEN: July 14th, 9 a. m.—1 p. m., See page 326

SESSION 3

Jointly with Sections CYT, GEN, and TPH: July 14th, 2—5 p. m., See page 330

SESSION 4

July 17th, 2—4 p. m.

Chairman: E. R. SEARS, Recorder: HEDDA NORDENSKIÖLD

SUBJECT:

Wild Populations, Discontinuity, and the Ecotype Concept

TYGE W. BÖCHER (Köbenhavn)
Cultivation Experiments with *Geranium*
Robertianum, *Veronica officinalis*, and
Prunella vulgaris

During the last ten years these three species have been used for a number of cultiva-

tion experiments combined with chromosome countings.¹ The present investigation was made for two main purposes: (1) A study of the

¹ T. W. BÖCHER in Dansk Bot. Arkiv Vol. 10 and 12 (1940, 1945), The New Phytologist Vol. 48 (1949) (*Prunella*), Dansk Bot. Arkiv Vol. 11 (1944) (*Veronica officinalis*), and Kgl. Danske Vidensk. Selsk. Biol. Meddelelser Vol. 20 (1947) (*Geranium Robertianum*).

distribution and occurrence in nature of races or characters as a contribution to general biological investigations of the species in question, (2) A study of the problem of continuous or discontinuous variation.

In *Geranium Robertianum* the variation seems to be discontinuous; the races could be referred to two main types, a wood type (var. *genuinum*), and a prostrate pebble beach type (var. *rubricaulis*).

In the two other species, however, the variation was almost entirely continuous. In *Veronica officinalis* there is a continuous increase in leaf size and this character gradient runs from oceanic to more continental regions and—although on a smaller scale—from unwooded to wooded habitats within the same area.

In *Prunella vulgaris* about 140 samples particularly from Europe have been cultivated. In this species an interesting distribution of a number of biophysiological characters was demonstrated. From north to south in Europe there is an increase for annuality and first year flowering and the same increase is found when comparing samples from wet, semi-wet, and dry habitats. Caespitose growth and early flowering seem to be characteristic of boreal or alpine races as well as Mediterranean races, while Central European lowland plants generally flower later and have a greater capacity for creeping.

In *Veronica officinalis* and *Prunella vulgaris* the most characteristic character combinations in the different habitats or climatic regions are called ecotypes. These ecotypes are in some way theoretical concepts as only rarely the ideal combination of characters is found in the same cultivation sample. The difference between such theoretical ecotypes and the more well-defined ecotypes found in other species may not, however, be great. Some species behave like *Geranium Robertianum*, where the ecotypes are very distinct and may be treated as taxonomical units. Other species have a continuous variation, which may be expressed in a number of clines,

and here the ecotypes are rather arbitrary ranges within these clines. Undoubtedly the behaviour of many species will be intermediate, and, consequently, theoretical and well-defined ecotypes cannot be kept apart, as we are unable to fix a limit between them.

Discussion

H. G. BAKER: I have been cultivating *Geraniums* of the Section *Robertiana* in Leeds for five years. Material of *G. Robertianum* from the British Isles shows well-defined ecological races in the same manner as the Continental material of Dr. BÖCHER. It may be that such races are common in the more Atlantic parts of Europe.

In Britain, the races parallel the 4n Continental races; thus there are prostrate shore forms and ascending woodland forms. In addition, the race originally described by OSTENFELD as *G. celticum* is a prostrate race from limestone in the more oceanic parts of the British Isles. Many colour forms of these races are found but these appear to lack ecological significance. Results so far indicate that the races are interfertile and therefore truly represent ecotypes of a single ecospecies.

Material from eastern U. S. A. has now been added to the cultures and included in the crossing-programme.

The very closely related *G. purpureum* VILL. is 2n and regularly annual. It forms a nearly sterile F_1 with *G. Robertianum* and therefore represents a separate ecospecies. It also has a prostrate shore-race in southern England together with an upright inland race.

F. EARNSHAW (Edinburgh)

The Nature of Ecotypes

An ecotype is defined as a plant population adapted by genetic specialisation to the physiological conditions of a particular habitat. There appear to be at least three prerequisites of ecotype formation:

- a) The species population must possess an

adequate potential range of genetic variability.

b) Growing conditions in ecologically distinct habitats must be sufficiently different to provide adequate selection potential.

c) Isolation between habitat populations must be sufficient to permit genetic specialisation.

Much genecological work has demonstrated ecotype formation in response to variation in major climatic factors. For example, CLAUSEN, KECK and HIESEY (1940) studied ecotype formation in *Potentilla glandulosa* along a 200 mile transect from coastal to alpine conditions in California. Four main ecotypes were distinguished and these were found to coincide with four taxonomic sub-species. This equation of ecotypes with taxonomic sub-species indicates that the processes of ecotypic differentiation have been complicated by migration and long continued isolation of the several stocks. Furthermore, there is no detailed study of ecotypic specialisation within the major ecotypes in response to variation of locally important factors.

SINSKAJA (1942) suggests that, within major (climatic) ecotypes, smaller populations, the ecoelements, may be distinguished. These are adapted to a particular level of a locally important ecological gradient. Since there is likely to be a recurrent series of such local gradients in successive climatic zones she envisages the ecotypic structure as a 'spirally overlapping series of analogous ecoelements.'

Ecotypic specialisation along these lines has been shown by GREGOR (1946) in populations of *Plantago maritima*. Here there was variation in both plant size and growth habit along an edaphic gradient. At a low level of soil fertility a decumbent habit was most common and plant size was smaller than in forms of similar growth habit which were a minor constituent of populations at higher levels of fertility. Conversely, erect forms were of larger size and more frequent on the more fertile soils. GREGOR has emphasised that each population must be influenced by a

complex of environmental factors, each capable of independent variation. He therefore considers it will be preferable to trace ecocline variation in response to particular ecological gradients, rather than to attempt to name local populations as distinct ecotypes. GREGOR also notes that separation by less than the probable distance of gametic dispersion, can provide sufficient isolation to permit genetic specialisation between neighbouring populations.

A fuller analysis of the processes of ecotypic specialisation seems to demand intensive field study to determine the population structure of particular species in relation to local ecological gradients. Such a survey should provide a basis upon which to sample populations for a detailed study of ecocline variation. Work along these lines has been begun in an area of hill vegetation near Edinburgh, where a few commonly occurring species are distributed over a range of ecological conditions in distinct types of floristic associations. It is hoped that this work will contribute towards a fuller understanding of ecotypic specialisation and towards a closer relationship between the viewpoints of the genecologist and the plant ecologist.

References

- CLAUSEN, J., KECK, D. D., & HIESEY, W. M. (1940). Experimental Studies on the Nature of Species. Publ. Carneg. Instn. No. 520.
GREGOR, J. W. (1946). Ecotypic Differentiation. New Phytol. 45, 254-270.
SINSKAJA, E. N. (1942). The Species Problem in Modern Botanical Literature. Usp. Sovrem. Biol. 15, 326-59. Translation by Dr. H. Fox, Comm. Agric. Bur., Cambridge.

Discussion

D. A. WEBB: The word "ecotype" is used in an ever-widening circle of meanings. This is inevitable, but important differences in interpretation of the questions at issue underlie the different uses. Some authors use the word so widely that it means simply a genetically distinctive, spatially isolated population;

others restrict it to denote a population that is morphologically distinctive; Dr. EARNSHAW wishes to restrict it to populations distinguished by characters, morphological or otherwise, which are closely adaptive with respect to the peculiarities of the environment. But do we know enough of physiological ecology to be able to discriminate these? We do not know, for example, in the case of most woodland plants, whether they are distinguished by demanding high atmospheric humidity, or by tolerating shade. The alpine environment is a complex difficult to analyse sufficiently to appreciate adaptation to it. Does Dr. EARNSHAW regard Dr. BÖCHER's examples of variation in leaf-size in *Veronica officinalis*, and in hairiness in *Geranium robertianum* as belonging to ecotypic variation?

F. EARNSHAW: In considering whether response is ecotypic it seems preferable to reserve the term ecocline for response to a clear ecological gradient. In absence of clear physiological gradient a non-committal term such as topo-cline is preferable.

D. D. KECK: The four subsp. of *Potentilla glandulosa* on the transect across central California are actually composed of two or more ecotypes each. Dr. EARNSHAW's definition of "ecotype" is acceptable as given but can one detect an ecotype as thus defined by looking for clines in single characters?

ALICE EASTWOOD: The serpentine areas vegetation in California—do other plants avoid it or do the serpentine plants want to monopolize it? There is a necessity of trying other plants in the serpentine soil.

A. D. BRADSHAW: The answer to the difficulty of knowing whether morphological differentiation is of ecological significance may lie in extensive cultivation experiments of the plant in habitat from which they originally came in order to see what survival there may be (as CLAUSEN, KECK & HIESEY). Work in progress on *Agrostis tenuis* has shown populations growing on lead-contaminated soils near lead mines to be distinctly more resistant to the contamination than plants growing nearby

on ordinary soil, although there is no morphological differentiation. This differentiation could only have been discovered by cultivation experiments. That the area on which this population is growing is only 70 yds. across supports Dr. EARNSHAW's suggestions to study local differentiation.

ANN-MARGRET PERJE (Stockholm)

The Variation within and between Clones in Ranunculus ficaria L.

In Sweden, *Ranunculus ficaria* is tetraploid. The chromosome number, determined from 20 different localities, is $2n=32$. The tetraploid form is highly sterile and the plant has mainly vegetative propagation with bulbils in the leaf axils. Cytological investigations show that at least 10 percent of the pollen is abnormal, that quadrivalents are found in meiosis and that the percent abnormal pollen grains can be explained by the irregular distribution of chromosomes. Sometimes night frost disturbs the premeiotic cell divisions, giving chromosome fragments and lagging chromosomes. In spite of some chromosome disturbances we nearly always get an 8-nuclear embryo sac of normal type. After this stage a degeneration begins. It is difficult to say if this disorganisation is due to a lack of fertilization or if it has set in though fertilization has taken place. Some of the ovaries swell, whereas others do not. Also in the big ovaries a disorganisation has taken place. Only in one case I have found an embryo in the seed. Meiotic irregularities cannot be the only cause of the reduced fertility. One assumption is that the embryo sacs or the zygotes are killed in the seed by physiological disturbances in the mother plant. MARSDEN-JONES and others have indicated that perhaps some hormonal substance, formed in the plant during the flowering time, impedes the growth. In the plant a growth-retarding substance, anemonin, is formed. This substance has long been known to retard the growth of yeast-

cells. In a preliminary experiment I have found a relatively high percent anemonin in the tetraploid plants. Thus it is possible that the plant itself produces such a high degree of anemonin or some other growth-inhibiting substance that the seeds cannot develop. An investigation is made to show how different quantitative characters vary inter and intra the clones. The following characters are investigated: the number of pistils, stamens, petals and sepals. The correlation of the increase in the number of stamens and pistils is determined. Plants from different clones have been cultivated in the same environment. Two years afterwards they have shown the same characteristics. Thus the differences are genetic and we can use the characters in describing different clones. As expected from an autotetraploid the stability of the populations is greater than in the diploid race. *Ranunculus ficaria* is another example of the rule that the autotetraploid form is more hardy and goes further north than the diploid one.

ROBERT K. VICKERY JR. (Stanford, Calif.)
An Experimental Study of the Races of the Mimulus guttatus Complex

This is an investigation of the genetic and ecologic barriers present between different races in the *Mimulus guttatus* complex (*Scrophulariaceae*). This complex consists of 16 closely related species distributed from Alaska to Southern Chile. These species contain numerous races which come from such diverse habitats as the sea-shore, foothills, high mountains, and the desert. They vary from 2 to 200 centimeters in height and may be annuals or perennials even within the same species.

A working collection of over 100 strains, representing the geographic range and morphologic diversity of the complex, is being grown in the Carnegie Institutions glasshouses at Stanford. Sixteen of the most diverse races are being studied intensively. These races come from a transect across central California, extending from the immediate sea-shore to the

crest of the Sierra Nevada at 3 000 meters elevation and to the Great Basin plateau beyond. In this group there are 5 *Mimulus* species: *guttatus*, *laciniatus*, *nasutus*, *Tilingi*, and *glabratus*.

The transect strains represent genetically distinct races since they retain their morphologic and physiologic individuality when grown under uniform conditions at Stanford.

These 16 strains were crossed in all possible combinations. The resulting hybrids are unfolding the following picture of the relationships in this sample of the complex.

1) All strains of *M. guttatus* hybridize readily, even tall perennials with tiny annuals.

2) There is no crossing barrier between *M. laciniatus* and *M. guttatus*, plants so unlike morphologically that they have always been considered to be specifically distinct. However, hybrid populations do occur naturally at the occasional points where their ranges meet.

3) *M. nasutus* and *M. guttatus* produce fully fertile hybrids. Their ranges coincide but the species remain apart because *M. nasutus* is pseudo-cleistogamous.

4) Crosses with alpine *M. Tilingi* rarely succeed but the rare F_1 's are fertile, hence there is an appreciable barrier between this species and the others.

5) *M. glabratus* crossed occasionally with the other transect races. It is the only species common to both North and South America.

6) Lastly, a typical race of *M. luteus* from the Andes crossed moderately well with the transect races from California, which indicates that the North and South American forms are still fairly closely related.

The crossing results plus several chromosome counts indicate that the chromosome number for the complex is probably $n=14$.

This experimental study shows that the *Mimulus guttatus* complex consists of many, clearly distinct races, all probably of the same basic chromosome number, and all partially or fully interfertile, but kept distinct by differences in mode or time of flowering, or by geographical isolation, or by partial genetic barriers.

SESSION 5

July 18th, 9 a. m. — noon

Chairman: IRENE MANTON, Recorder: G. TURESSON

SUBJECT:

Origin and Development of Wheat and Barley

E. R. SEARS (Columbia, Mo.)

The Origin and Evolution of the Wheats

The genera of the wheat group—*Triticum*, *Aegilops*, *Agropyron*, *Secale*, and *Haynaldia*—are generally assumed to have evolved from a common ancestor with seven pairs of chromosomes. In the genus *Triticum* two divergent forms, probably from different genera, combined to give rise to the tetraploid wheats, and a third form was then added to produce the hexaploid wheats. This third form has now been identified as *Aegilops squarrosa*. Of the other two forms, one was presumably a diploid *Triticum*, and the other may have been an *Agropyron*. Synthetic hexaploid wheats, produced by adding the chromosomes of *Ae. squarrosa* to various tetraploid wheats, indicate by their behavior in hybrids with naturally occurring hexaploids that few changes have taken place in the natural hexaploids since their origin. The tetraploids, on the other hand, have evidently undergone many changes since they first arose.

A method is now available for discovering some of the changes which have taken place in the chromosomes during the process of evolution of the wheats and their component species. This method makes use of the nullisomics, tetrasomics, and related aberrations which have been obtained in common wheat. Combinations of two monosomes show whether or not the two chromosomes concerned can pair with each other. Combinations of tetrasomes with nullisomes indicate genetic homology if the extra dosage of the one chromosome tends to compensate for the deficiency of the

other. One series of three related chromosomes has been identified. Three series of two have also been established, in each of which a third member has been tentatively identified. Thus it appears that at least some of the chromosomes have retained much of their individuality throughout the evolutionary process.

The nullisomes and tetrasomes may possibly be used also for studying the mutations that have occurred in polyploid wheat but which are partly or wholly obscured by duplicate loci. Where a series of three homologous chromosomes has been identified, plants tetrasomic for one chromosome of the series and nullisomic for the other two may presumably be obtained, and in these plants mutant genes on the tetrasomic chromosome will be free to express themselves.

ELISABETH SCHIEMANN (Berlin-Dahlem)

Ursprung und Entwicklung von Weizen und Gerste

Es soll versucht werden, die im letzten Jahrzehnt von deutschen und ausserdeutschen Botanikern und Genetikern gelieferten Beiträge zur Phylogenie von Weizen und Gerste zur Synthese zu bringen, besonders die Resultate der in der ausserdeutschen wissenschaftlichen Presse wenig bekannten deutschen Arbeiten in den Gesamtrahmen einzuspannen. — Diese Beiträge betreffen:

- 1) Materialbeschaffung durch eine Reihe von grossen Expeditionen, die alle nach Innerasien gingen; 2) die Auswertung dieses Materiales, das a) für die Phylogenie des Weizens b) der Gerste wichtig geworden ist; 3) die

nomenclatorische Bereinigung der Getreidenamen; 4) die Bearbeitung neuen Ausgrabungsmaterials, a) aus dem Orient; b) aus Deutschland.

Es werden die Weizenstammbäume von VAVILOV, FLAKSBERGER, SCHIEMANN und BERTSCH besprochen. Dafür ist eine Auseinandersetzung mit VAVILOVs Anschauung über die sog. „Wildgetreide“ notwendig, die zu einer Stellungnahme gegenüber der Genzentrentheorie führt. Diese wird am Beispiel der Phylogenie des Weizens und der Gerste durchgeführt.

Es ergibt sich, dass abweichend von VAVILOV für die Weizen als primäres Mannigfaltigkeitszentrum = Ursprungszentrum, sowohl für die tetraploiden wie für die hexaploiden Weizen, Vorderasien bis Transkaukasien anzusehen ist, während Abessinien für die tetraploiden, der Hindukusch für die hexaploiden Weizen ein sekundäres Stauungszentrum bildet.

Bezüglich der Gersten haben die deutschen Expeditionen und die im Anschluss durchgeführten Literaturstudien ganz neue Gesichtspunkte gebracht. Die von ÄBERG 1938 für Tibet neubeschriebene 6-zeilige Wildgerste *Hordeum agriocrithon* ist seither von deutscher Seite zweimal wieder nachgewiesen worden. FREISLEBEN († 1945) kam auf Grund der Ergebnisse der Expeditionen, besonders der Deutschen Hindukusch-Expedition, zu der Annahme, dass die zweizeilige Kulturgerste, welche erst westlich des Hindukusch auftritt, dortselbst im Kontakt der von Osten als Kulturgetreide einwandernden 6-zeiligen Gerste mit der wilden 2-zeiligen, *Hordeum spontaneum*, hybrid entstanden ist.

Damit wird das ostasiatische Genzentrum der Gerste ein Primärzentrum für die 6-zeilige Gerste, Mittelasien das Ursprungszentrum der 2-zeiligen Gersten, und Abessinien auch für die Gerste, 2- wie 6-zeilige, ein sekundäres Stauungszentrum.

In einem zweiten Teil folgt eine Auseinandersetzung mit der von McFADDEN und SEARS 1948 in Stockholm vorgetragenen Ableitung der hexaploiden Weizen auf Grund der Syn-

these von *Triticum spelta* aus *Triticum dicoccoides* × *Aegilops squarrosa*. Es werden die problematischen an diese Synthese geknüpften weiteren Hypothesen auf ihre Wahrscheinlichkeit hin geprüft. Die von BERTSCH vertretene Phylogenie der Weizen wird abgelehnt und offene Probleme herausgearbeitet.

Discussion

E. R. SEARS: The theories given in the McFADDEN-SEARS paper are largely those of Mr. McFADDEN, who unfortunately is not here. I should only like to point out that one difficulty in assuming that *Triticum spelta* arose secondarily from free-threshing wheat is that people would not have been likely to select *T. spelta* if they already had *T. vulgare*.

E. SCHIEMANN: Es ist unwahrscheinlich, dass der mit dem Emmer im Neolithikum der Pfahlbauten vorkommende kompakte Nacktweizen tetraploid war, weil der hexaploide in unserer Zeit gerade da (und fast nur da) vorkommt, wo

1) im Neolithikum Einkorn und Emmer gebaut worden sind oder 2) noch bis heute gebaut werden oder bis mindestens vor 30-50 Jahren gebaut worden sind; so

1) in Schweden

2) in Schweiz, österr. Alpen, Süddeutschland, Thüringen.

Es ist wahrscheinlicher, dass es kontinuierlich derselbe Weizen war, als dass der tetraploide, als Nacktweizen durch den hexaploiden gleichartigen Nacktweizen ersetzt wurde, während Einkorn und Emmer blieben.

W. RUDOLF: I might question whether Mrs. SCHIEMANN is of the opinion that in her hypothetical phylogeny *T. boeoticum* was crossed with *Agropyrum triticeum* to originate the tetraploid *Spelta* wheat. Mrs. SCHIEMANN denies she knows and Dr. SEARS acknowledges that the ± homology of the genom of *A. triticeum* has not yet been able to be proved with the B genoms in the tetraploid and hexaploid wheats.

E. SCHIEMANN: Die Kreuzung *Triticum*

monococcum \times *Agropyrum triticeum* ist ganz hypothetisch von McFADDEN und SEARS angenommen und ist noch nicht ausgeführt worden, weil das lebende *Agropyrum*-Material fehlt.

E. R. SEARS: We have been unable to cross *Agropyrum triticeum* with Einkorn in the few attempts we have made. After having *A. triticeum* for a time, we lost it, but now have again what we believe to be *A. triticeum*.

ÅKE GUSTAFSSON: We must attach very great importance to the historical and phyto-geographical data that *Triticum spelta* is a derived type. Maybe it arose as a mutation. My colleague, Mr. MAC KEY, has obtained X-ray speltoid mutations that are very much alike to *Triticum spelta*, even more so than spontaneous speltoids.

J. MAC KEY: Is it necessary from a plant geographical point of view to consider the primitive tetraploid wheats to have spelted glumes? If the naked types are the most primitive ones the spelted types (*dicoccoides*, *dicoccum*, etc.) could be mutations with about the same mechanism in their occurrence as *T. spelta* and speltoids out of the naked hexaploid *T. aestivum*. Thus there would be a parallelism in differentiation in the emmer and in the hexaploid group.

E. SCHIEMANN: Von historischem Gesichtspunkt aus halten wir die tetraploiden Spelzweizen für die ältesten (Neolithicum v. Ägypten, Vorderasien und Europa). Tetraploide Nacktweizen sind erst von römischer Zeit in Ägypten bekannt.

E. R. SEARS: It is unlikely that compactness in the tetraploid wheats is due to the same gene as causes compactness in the hexaploids, for this gene is in the D genome. It may be that compactness of the tetraploids is caused by the squarehead gene on chromosome IX, the speltoid chromosome. The D genome, coming from the lax *Ae. squarrosa*, tends to lengthen the spike, so in the tetraploids, which lack this genome, the squarehead gene ought to have a greater effect.

E. SCHIEMANN: Es ist noch nicht genetisch geprüft ob das *compactum*-Gen von tetra-

und hexaploiden Weizen übereinstimmend das C-Gen von NILSSON-EHLE (1911) ist. Squarehead- und kompakte Typen kommen in beiden Polyploidstufen vor.

EWERT ÅBERG (Uppsala)

Studies on the Origin and Classification of Barleys and their Significance for the Principles in Classification of Selfpollinated Cultivated Plants

On the basis of studies which started with barleys from Eastern Tibet, problems of origin and classification of cereals, mainly barley, were discussed in earlier publications (ÅBERG 1940, 1948; ÅBERG and WIEBE 1946, 1948). These problems were recently brought under discussion again as a result of an investigation by BRÜCHER on barleys from the German SCHÄFER Expedition in 1938-1939. The details from BRÜCHER's investigation together with conclusions from his investigation and the author's publications on the material collected by SMITH in 1934-1935 have been brought together in a recent paper (BRÜCHER and ÅBERG 1950).

Origin. The rôle of Central Asia for the development of cultivated plants is very little known. After the discovery of a six-rowed brittle barley, *Hordeum agriocrithon*, from Eastern Tibet (ÅBERG 1938) there has been greater interest for the importance of this part of the world in respect to the origin of barleys. As early as in 1939, SCHIEMANN came to the conclusion that there is a need for studies of the barleys in the area between Eastern Tibet and Southwestern Asia, i.e. in Central Asia. FREISLEBEN (1940) expressed similar views and he also discussed a new discovery of *Hordeum agriocrithon* (1943) from the Tibetan area. It is of special interest that BRÜCHER has found two biotypes, which closely resemble *Hordeum agriocrithon* and only in minor characters differ from it. On the basis of the author's earlier theories (1940, 1948) and those of SCHIEMANN, FREISLEBEN and BRÜ-

CHEER there is good reason to believe that the great variation in the material from Eastern Asia is also likely to occur west of there, in other words in the region of Central Asia, and that therefore the rôle of Central Asia for the origin of cultivated plants is more important than earlier anticipated. This does not entirely agree with VAVILOV's theories (1926) but does not necessarily oppose them. It only brings out the necessity of studying the original material in the isolated regions of Central Asia with special emphasis (1) on the possibilities for a genetic change from wild forms with brittle rachis to cultivated ones with tough rachis—in accordance with DE CANDOLLE's theories in 1884—and (2) on the environmental influence on genetically unstable plants under especially favourable climatic conditions—in accordance with VAVILOV's theories in 1926. A combination of the theories of these two scientists is necessary for the right understanding of the development of plants in Central Asia as well as in other parts of the world.

Classification. The significance of the studies on Tibetan Barleys for the classification of cultivated selfpollinated plants is striking mainly because of the possible evaluation of characters useful for classification. The studies have proven that the taxonomist who is working with cultivated plants, which as a rule can be classified only with the help of minute characters, must be concerned with the diversity of morphological characters of species as well as of subdivisions of the species. He must carry out his studies with the help of experimental plots in the field and he must place his experimental plots under different environmental conditions. (ÅBERG 1943, ÅBERG and WIEBE 1948). The modern trend in classification of cultivated plants ought to

be that the best possible use should be made of all observable characters by studying them at a number of stations and in different years. It is very important to keep in mind that the material to be studied is a living material. By giving full credit and attention to numerous varying characters as well as to the stable ones it is possible to arrive at a more complete description.

In the above-mentioned paper by BRÜCHER and ÅBERG (1950) the opinion is expressed that new varieties should not be named and described. As a result, questions of species limitations and terminology, which were discussed by ÅBERG (1943), are again brought up for discussion. It is suggested in the paper just mentioned that for classification of selfpollinated cultivated plants three groups should be used. The first two groups, namely "species" and "variety", should carry Latin names, the third one, the "biotype", should have no Latin name. A revision of the material available in barley collections the world over would undoubtedly lead to a simplification of the present systems and correspond to what the present situation in a cultivated plant of the type of barley calls for.

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SESSION 6

Jointly with Sections AGR, CYT and GEN: July 18th, 1—4 p. m., See page 174

SESSION 7

Jointly with Sections CYT, GEN and TPH: July 19th, 9 a. m. — 1 p. m., and 2 — 5 p. m.

Chairmen: R. E. CLELAND, T. W. BÖCHER, Recorder: A. MÜNTZING

SUBJECT:

Taxonomical Units in Relation to Cyto-Genetics and Genecology

DAVID D. KECK (Stanford, Calif.)

Examples of the Applications of Experimental Methods to Taxonomy

Inherent relationships in plants can be studied by experimental methods, and upon a knowledge of them a natural classification can be based.

Members of the *Achillea millefolium* complex are morphologically difficult to separate but they have physiological and cytological differences that can be analyzed. Members of this complex occur in most of the major environmental niches available to land plants in California, from sea level to alpine heights in the Sierra Nevada. They occur as climatic races or ecotypes within two genetically distinct species which are separated by a difference in chromosome number.

Members of the polymorphic species *Potentilla glandulosa* occupy nearly as many environments in California as the *Achilleas*, but in this instance the species is composed of four morphologically well-marked subspecies, each with altitudinal ecotypes differentiated within it.

In the genus *Layia* with fourteen species all of which occur in California, the pattern of distribution is quite different, for all occur in the lowlands almost exclusively. Physiological differences are unimportant as compared with *Achillea* and *Potentilla*, but morphological differentiation is marked. Chromosome number is also important. The most pronounced genetic discontinuities in *Layia*, however, are not coincident with the major morphological breaks. For instance, a species

previously unrecognized and confused with two others with which it has a number of morphological characters in common, in fact is the genetically most distinct one in the genus — a monotypic cenospecies.

To recapitulate: in *Achillea* in California there are many climatic races which are physiologically well differentiated but morphologically less distinctly so; in *Potentilla glandulosa* the range of environments occupied is nearly as wide as in the case of the *Achillea*, but the subspecies are strongly marked and morphologically they resemble species; they contain ecotypes, but the number of climatic races is reduced; in *Layia* the genus covers only a fraction of the environments of the other two, and the pattern is one of numerous ecospecies aggregated into cenospecies and having few ecotypes.

Discussion

D. H. VALENTINE: When alpine and lowland subspecies of *Potentilla glandulosa* are crossed, do you find that the set of seed is as good, both quantitatively and qualitatively, as in crosses within the subspecies? It seems possible that slight genetical barriers might be demonstrated in a lower set of seed in the intersubspecific crosses. And have you made any genetical investigations on the *P. glandulosa* complex in other parts of its range, outside the Californian transect?

D. D. KECK: No genetic barrier thus far detected between the subspecies of *Potentilla glandulosa*, although the possibility is not excluded that an incipient barrier is present.—

Other forms of *P. glandulosa* have been studied and classified although their genetical relationships to the subspecies occurring on the California transect have not been tested by crossing.

J. LANJOUW: Is the method used by Dr. KECK and collaborators for species and lower categories also applicable to genera and higher categories?

D. D. KECK: The cenospecies line appears to mark the limit for experimental attack on the problem of relationships. If no possibility exists of linking groups genetically, the closeness of their relationship can only be guessed at. Therefore experimental methods are not yet applicable to determining family relationships.

N. W. SIMMONDS: Does isolation occur at the F_2 level in any of the groups mentioned? This is known in cotton where the F_1 is vigorous and fertile but the F_2 weak.

D. D. KECK: The F_2 generation is the most significant in determining genetic barriers as in the cross *Layia gaillardoides* \times *L. hieracioides*, for these barriers often fail to show up in the F_1 plant which may even be highly fertile.

N. H. BRITTAN (Hull)

*Cytotaxonomy of some species of
Agrimonia L.*¹

The genus *Agrimonia* L. is represented in the British Isles by two species—*A. eupatoria* L. and *A. odorata* (GOUAN) MILL. The morphological differences are slight and are represented by fruit and leaf indumentum characters. Of these the fruit characters are the more definite. An obconic, furrowed calyx tube surmounted by a ring of erect and patent spines is found in *A. eupatoria*, whereas in *A. odorata* there is a smooth, campanulate calyx tube with reflexed spines in addition to the erect and patent ones. The leaf character is rather more variable, the indumentum of the underside in *A. eupatoria* consists of a

dense covering of clothing hairs interspersed with multicellular hairs; in *A. odorata* there are fewer clothing and multicellular hairs, and in addition large, stalked, glandular hairs occur.

Cytologically the two species are quite distinct, all plants of *A. eupatoria* which have been examined have been found to have a somatic complement of 28 chromosomes, and *A. odorata* 56. Both are fertile and produce abundant seed, the regular reduction division which this suggests has been found in both species.

The chromosome numbers suggest a polyploid series and in view of the fertility of the higher-numbered member, allopolyploidy is probable. In order to prove this reciprocal crosses were attempted. These did not produce the required hybrid plant, but one with $2n=14$ was obtained. It is hoped to obtain confirmation that the base number of the genus is 7 from an investigation of meiosis in this plant.

A sterile plant found in a locality where *A. eupatoria* and *A. odorata* grow together, was found to have $2n=42$, suggestive of hybrid origin. Its meiotic division has not yet been fully investigated but its pollen shows some 37 % abortive grains, and the size-frequency distribution of the good grains shows a smaller mean length and wider deviation than either putative parent. These facts suggest that allopolyploidy has in fact been responsible for the production of *A. odorata*.

The following previously unpublished chromosome counts have been made:

$2n=28$:—*A. repens* L., *A. pilosa* LED.,

$2n=56$:—*A. grypsosepala* WALLR., *A. striata* MICHX.

GUSTAV A. L. MEHLQUIST (St. Louis, Mo.)
*Inheritance in Delphinium Hybrids between
D. Cardinale Hook. and D. elatum L.*

In order to produce perennial red- or pink-flowered delphiniums, crosses were made in

¹ Abstract of paper submitted but not read.

1942 between a colchicine-induced tetraploid of the red-flowered *D. cardinale* Hook. ($2n=16$) and a white-flowered garden form of *D. elatum* L. ($2n=32$). The fifteen F_1 plants were all tetraploid ($2n=32$), purple-flowered, and in habit of growth rather close to *D. cardinale*. Five of the plants were ovule-sterile but partially pollen-fertile, the others were partially fertile on both sides. Meiosis was irregular with from 8 to 16 bivalents and the rest univalents. Frequently, both anaphase I and II showed one or two chromatin bridges and fragments. No cytological differences could be seen between the ovule-sterile and partially fertile plants.

Back-cross hybrids with forms of *D. elatum* were readily obtained, all of which were tetraploid. In habit of growth they were intermediate between the F_1 and *D. elatum*. Nine out of a group of 154 were pale lavender-blue, all the others were purple. Meiosis was more irregular than in the F_1 and but few seeds resulting in two seedlings have been obtained over a period of six years.

In an F_2 population of 349 plants 7 were intermediate in flower color between *D. cardinale* and the F_1 and 14 were intermediate between the F_1 and the white-flowered parent. There were no reds or whites. However, pink- and red-flowered segregates appeared in the F_3 and F_4 , indicating that some allosyndetic pairing had taken place. All the pink- and red-flowered segregates were similar to *D. cardinale* in habit of growth but none was so intensely colored as this species. They were all seed-sterile but could be used as pollen parents in back-crosses to *D. elatum*. All such back-cross progeny were purple-flowered regardless of the color of the *D. elatum* forms used as seed parents. In habit they were essentially intermediate. They were highly seed-sterile but some could be used as pollen parents in further back-crosses.

In the second back-cross of these red and pink segregates to white-flowered *D. elatum*, 47 plants were obtained consisting of 9 purple, 24 lavender, and 14 white.

Some of the purple-flowered segregates from these crosses were back crossed two or more generations to various forms of *D. elatum* resulting in purple-flowered hybrids that are similar to this species in habit of growth and fairly self-fertile. Further work will determine whether pink- or red-flowered segregates suitable for garden planting can be obtained from these hybrids. Even if segregation for pink or red occurs, it may be necessary to go through a second back-cross series with *D. elatum* in order to obtain plants suitable for garden planting. If no pink or red segregates are obtained, back-crosses will be made to red-flowered derivatives from the F_1 lines and then again back to forms of *D. elatum* in order to regain the fertility and habit of this species before selfing is undertaken.

ANTERO VAARAMA (Piikio, Finland) *Cytotaxonomic Studies on Northern Tripleurospermum Forms*

This investigation is an attempt to elucidate the taxonomy of the Fennoscandian forms of the collective species *Tripleurospermum* (= *Matricaria*) *maritimum* (Koch) Hyl. with the aid of cytological observations. Taxonomy based only on morphological analysis encounters great difficulties. It has not led to sufficiently satisfactory results. The checking of the herbarium material from the most important Fennoscandian collections has been carried out side by side with cytological investigation.

The morphological and cytological observations made have led to the following classification:

Tripleurospermum maritimum

ssp. *inodorum* (L.) Hyl.

ssp. *salinum* (WALLER.) comb. nov.

ssp. *ambiguum* (Fr. & Sav.) comb. nov.

Ssp. *inodorum* is relatively monotypic in Fennoscandia. In the other subspecies the

following smaller taxonomic units can be distinguished:

ssp. salinum

var. *raji* (NEUMAN) comb. nov.

var. *recentiorum* (NEUMAN) comb. nov.

var. *gotlandicum* var. nov.

ssp. ambiguum

var. *nanum* (POLUNIN) comb. nov.

var. *boreale* (HARTM.) comb. nov.

var. *litorale* var. nov.

var. *villosum* var. nov.

The *ssp. inodorum* is tetraploid ($2n=36$). The chromosome morphology reveals its amphiploid origin. It is a typically anthropochorous plant greatly favoured by the increase in intensive agriculture.

Ssp. salinum is a diploid form group ($2n=18$). It is a halophilous ecotype of sea-shores. It occurs only occasionally in ruderal habitats. Var. *raji* has a very clear distribution centre along the shores of Bohuslän and Halland in Sweden. The range of the var. *recentiorum* is wider. It grows on the shores of the Southern Baltic, the North Sea and the Atlantic. Var. *gotlandicum* has its centre in the islands of Öland and Gotland.

Except the var. *villosum* which is hexaploid ($2n=54$), *ssp. ambiguum* is diploid ($2n=18$). The range of the form group is circumpolar, both arctic and subarctic. It grows commonly in ruderal habitats. In the beginning of this century the southern border of its area in Fennoscandia reached Scania in Sweden and the Skagen peninsula in Denmark. Now this picture has apparently changed. The frequency of the subspecies has greatly diminished especially in the southern part of its area by introgressive hybridization with the dominant subspecies *inodorum*.

The variety *nanum* belongs to the high arctic. Var. *litorale* is a sea-shore type of the northern Baltic and the White Sea. Var. *boreale* is an interesting type growing mainly on the hill slopes of Kullen in Scania and Bornholm.

The diploid forms hybridize easily with one

another. Various combinations between the characters of the different forms can be found abundantly in nature. *Ssp. inodorum* hybridizes with both the other subspecies. The fertility of triploid hybrid is, however, weak. In the F_2 -generation only aneuploid individuals have been observed.

PETER BERNSTRÖM (Lund)

Species Relationships in Lamium

The old question about the real nature of *Lamium intermedium* and *L. hybridum* and their systematic position in relation to *L. purpureum* and *L. amplexicaule* has been investigated. *Purpureum* and *amplexicaule* are diploid ($2n=18$), whereas *intermedium* and *hybridum* are tetraploid ($2n=36$). The only hybrid combination obtainable of the 6 possible ones is that between *hybridum* × *amplexicaule*, the hybrids being triploid and completely sterile. However, by using artificially produced tetraploids of *purpureum* and *amplexicaule*, where the use of the diploids has failed, the following 4 new kinds of hybrids have been obtained: tetraploid *purpureum* × diploid *amplexicaule*, *hybridum* × *purpureum*, *intermedium* × *purpureum* and *intermedium* × *amplexicaule*. By studies on the chromosome pairing at I M of all kinds of hybrids available, in connection with genetical studies on the offspring of some of them, it has been possible to prove that both the tetraploid species are amphidiploids, and that the parent species to *L. intermedium* are *L. purpureum* and *L. amplexicaule*, while those of *L. hybridum* probably are *L. purpureum* and some other species, the genom of which is rather homologous with that of *L. amplexicaule*. For taxonomical reasons this component of *L. hybridum* is supposed to be *L. bifidum* from the Balkans. The origin of *L. intermedium* is demonstrated by the synthesis of this species in two different ways. Indications are found that this species is a young one from a biological point of view.

AXEL NYGREN (Uppsala)

Biotype and Species Formation in Some Grass Genera

In *Calamagrostis* amphimictic as well as apomictic species occur. The species in Europe most rich in biotypes is *C. purpurea*, which has chromosome numbers varying between $2n=56-91$. *Purpurea* is diplosporous and develops normally no pollen in the anthers. Among 174 investigated clones, one had pollen in the spikelets of the older panicles, but not in the younger panicles of the same plant. The older panicles had also sexual E.Ss. This clone ($2n=56$) was crossed with different amphimictic species ($2n=28$); the hybrids as a rule had $2n=70$. The hybrids resembled the mother *purpurea* clone and had diplosporous as well as sexual E.Ss. In F_2 there was a segregation in three offsprings out of 37, i.e. in crosses with *arundinacea*, *canescens*, and *epigeios*. The F_2 -plants have diplosporous and sexual E.Ss. as well. Morphologically they combine the characters of the parents in different ways. *Purpurea*-plants with pollen have also been obtained in some offsprings from bagged mother plants with $2n=56$. 673 descendants were raised of forty clones; in all, 31 plants belonging to eight clones with pollen were obtained. These descendants had $2n=56$, and developed diplosporous as well as sexual E.Ss. They were bagged and also crossed with amphimictic species. Some offsprings from these baggings showed segregation, while others were non-segregating. Different panicles on the same plant behaved differently in this respect. The descendants in the segregating offsprings as a rule had higher chromosome numbers than the mother plant, while the descendants in the non-segregating ones had the same number. Morphologically the former often deviated obviously from the mother clone.—In *Poa* the species *Poa arctica* R. Br subsp. *caespitans*, *depauperata*, *elongata*, *microglumis*, and *stricta* have been studied as well as *Poa laxa* subsp. *flexuosa*, viviparous as well as non-viviparous *Poa pratensis* subsp.

alpigena, at the same time as the hybrids between *Poa alpina* and *arctica*, *alpina* and *laxa flexuosa* (= *Poa jemlandica*), and *alpina* and *pratensis alpigena* (= *Poa herjedalica*). *Flexuosa* is a sexual with $2n=42$, the different *arctica* subspecies are aposporous to a high extent with the exception of the viviparous *stricta*, which seems to be a lost remnant of an old sexual population. The hybrid *herjedalica* has aposporous, diplosporous, as well as sexual E.Ss. in different biotypes, but aposporous and diplosporous sacs never occur together in the same plant.

The abundance of forms occurring in *Calamagrostis purpurea*, *Poa arctica*, *P. pratensis*, and the hybridogenous *P. herjedalica* have originated by crossing between different biotypes, some of which have been sexual or semi-amphimictic, while others have been apomictic. In this way the genes for apomixis have been spread in the vast populations, composed by all ecospecies belonging to the same coenospecies. In such a complex a cross between two amphimicts might give an apomict as often as the combination amphimict \times apomict or apomict \times apomict will give a sexual. In later generations, however, there will be a recombination of the type of reproduction occurring in the parents. Because of the combination between sexuality and apomixis the number of types formed will be enormous and thus *Calamagrostis purpurea* as well as the *Poa*-species and hybrids mentioned are complexes in being.

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- 1951. Form and biotype formation in *Calamagrostis purpurea*.—*Hereditas* 32, pp. 519–532.

HEDDA NORDENSKJÖLD (Uppsala) *Cyto-Taxonomic Studies in the Genus Luzula*

An inventory of the species of the genus *Luzula* has been made. Circa 30 species have been examined. By the investigation of the somatic chromosomes the following results have been obtained: Almost half the number of species studied are characterized by having 12 chromosomes. Those chromosomes have at metaphase a length of about two μ and a uniform thickness of about half a μ in the fixatives used. They show no constrictions. This chromosome type will be called the standard chromosome type of the genus *Luzula* and the chromosomes of that size will be denoted the AL-size. The other species of the genus investigated have more numerous but at the same time smaller chromosomes. The species with smaller and more numerous chromosomes are found in different sections of the genus and are usually closely related to species with 12 chromosomes of the standard type. The only species examined with larger chromosomes than that of the standard size is *L. purpurea*, and this species has only six chromosomes somatically. There often seems to be a certain relationship between the number and the size of chromosomes in different species. When the number of chromosomes is doubled from 12 to 24 the length of the chromosomes is reduced to about half the standard length. This smaller type of chromosomes has been called the BL-size. Some species with 48 chromosomes have a chromosome size of about half the BL-size, and are referred to as having the CL-size. Those chromosomes are almost spherical at metaphase stage. Further reduction of chromosome size is met with in connection with increased chromosome number, but here the chromosomes are too small to allow any detailed examination.

Most of the species have throughout the same chromosome size in the cells. In some cases, however, different chromosome types are found in the cells of some species. This phenomenon is often connected with an aneu-

ploid chromosome number. As an instance, there is a species belonging to the *campestris-multiflora* complex which has two different races with different chromosome numbers, which both are aneuploid. The chromosome numbers are somatically: 1) 22 with 2 chromosomes of the AL-size and 20 of the BL-size, 2) 20 with 4 chromosomes of the AL-size and 16 of the BL-size. In the subgenus *Pterodes* of the genus *Luzula* several species have an aneuploid chromosome number with unequal sizes of the chromosomes in the cells. But here the chromosomes are usually very small and thus it is impossible to make a more detailed cytological examination. In some cases, however, we have large and small chromosomes in the same cells in spite of an euploid chromosome number. This fact might indicate some kind of hybrid origin. We have for instance *L. arcuata* with 36 chromosomes somatically, 12 of which are of the AL-size and 24 of which are of the BL-size.

When closely related species with chromosomes of different sizes are crossed with each other the chromosomes of the hybrids maintain the size of their parents and it is possible to determine from which of the parents the chromosomes originate. Hybrids of that type which have been investigated (*L. campestris* \times *L. sudetica* and *L. pallescens* \times *L. sudetica*) had 6 chromosomes of AL-size and 24 chromosomes of CL-size. The different types of chromosomes were very distinct at the somatic division and the size relation of the chromosomes from the parents are kept in the cells of the hybrids. At first metaphase the six large chromosomes of AL-size do not pair with each other but with several of the small chromosomes. The rest of the small chromosomes, which are not attached to the large ones, remain univalents and do not pair with each other.

The species of the genus *Luzula* which have been examined as to their somatic chromosomes are as follows:

<i>Subgenus Anthelaea:</i>	2n
<i>L. purpurea</i> LINK	6
<i>L. silvatica</i> (HUDS.) GAUD.	12

<i>L. lutea</i> (ALL.) DC.....	12
<i>L. luzuloides</i> (LAM.) DANDY et WILM.	12
<i>L. nivea</i> (L.) DC.	12
<i>L. Henriquezii</i> DEG.	12
<i>L. parviflora</i> (EHRH.) DESV.	24
<i>L. Wahlenbergii</i> RUPE.	24
<i>L. subcongesta</i> JEPS.	24
<i>L. glabrata</i> DESV.	12
<i>L. spadicea</i> (ALL.) DC.	12
Subgenus <i>Pterodes</i> :	
<i>L. Forsteri</i> (SMITH) DC.	24
<i>L. Luzulina</i> (VILL.) D. T. et SARNTH	24
<i>L. Johnstonii</i> BUCH.	42
<i>L. rufescens</i> FISCHER	52
<i>L. acuminata</i> RAF.	48
<i>L. pilosa</i> (L.) WILLD.	66
Subgenus <i>Gymnodes</i> :	
<i>L. arctica</i> BLYTT	24
<i>L. arcuata</i> (Wg) SW. coll.	36, 42
<i>L. spicata</i> (L.) DC.	12, 14, 24, 36
<i>L. abyssinica</i> PARL.	24
<i>Campestris-multiflora</i> complex:	
<i>L. campestris</i> (L.) DC. s. str.	12
<i>L. pallescens</i> SW.	12
<i>L. echinata</i> (SMALL) HERM.	12
<i>L. bulbosa</i> (WOOD) RYDB.	12
<i>L. comosa</i> v. <i>macrantha</i> WATS.	12
<i>L. comosa</i> v. <i>laza</i> BUCH.	12
<i>L. campestris</i> v. <i>columbiana</i> ST. JOHN	12
<i>L. sudetica</i> (WILLD.) DC.	48
<i>L. orestra</i> SHARSM. (ined.)	20, 22
<i>L. groenlandica</i> BÖCHER.	24
<i>L. comosa</i> E. MEY. s. str.	24
<i>L. multiflora</i> (RETZ.) LEJ.	24, 36
<i>L. frigida</i> sensu SAMUELS.	36
<i>L. congesta</i> (THUILL.) LEJ.	48

This investigation is published in detail in *Hereditas* 37 (1951) pp. 325-355.

ÁSKELL LÖVE (Reykjavik)

The Taxonomical Evaluation of Types with Different Chromosome Numbers

The taxonomical significance of differences in the number of chromosomes is first and

foremost a question of definition of the taxa. According to almost all modern and classical taxonomists the taxonomical system should coincide as much as possible with the biological systems of nature. Biologically more or less strongly isolated natural groups of the lowest rank are classified as separate species, the higher ranks of isolated groups being genera, families, etc. Within this lowest biologically isolated unit subgroups are met with, but although morphologically, geographically, or ecologically more or less clearly separable, they are always inter fertile and perhaps comparable with the different races of mankind. Major geographical races are classified as subspecies, minor geographical races or local facies are placed as varieties, and morphologically recognizable types within these subgroups, without clear geographical area but appearing here and there, are named as forms. Ecological variations, which may or may not be morphologically distinct, are classified as ecotypes. They are sometimes found to be identical to some of the geographical races mentioned, but most often corresponding ecotypes may be met with in different geographical races. The intraspecific units are almost never without intermediate types but connected by a series of clines. These are, however, not met with between good species, although introgression might cause the occurrence of some morphologically intermediate types in some species groups with weak possibilities of hybridization.

If these taxonomical definitions were really accepted and practised by all botanists, the so-called "intraspecific chromosome races" of the cytologists would never be accepted by taxonomists, as differences in chromosome number without exception reveal a very strong barrier of sterility. Types with different chromosome numbers are, further, never connected by a clinal variation, and they are never classifiable only as ecotypes, although they always are ecologically distinct. Due to their sterility barrier, such types are not classifiable as subspecies or varieties only, and

the only taxonomical group they should be classified into is that of separate species.

Some types found to differ from each other in the number of chromosomes are not very clearly distinct morphologically. Based on this fact, cytologists have often declared that they were not separable at all, and several taxonomists seem to have accepted this as a clear demonstration of the real occurrence of "intraspecific chromosome races." In reality, this opinion is not based on the fact that varying chromosome numbers may be met with in morphologically completely indistinguishable types, but it is rather the result of the varying taxonomical interest and ability of the cytologists, as shown, e.g., by the fact that although so-called "intraspecific chromosome races" have been reported within about 10 per cent of the species of Northwestern Europe, almost all these "races" have previously been described as separate species by classical taxonomists. Some of the most striking examples are: *Phleum pratense*: *nodosum*, *Ph. alpinum*: *commutatum*, *Dactylis glomerata*: *Aschersoniana*, *Dactylorhiza maculata*: *Fuchsii*, *Acetosella vulgaris*: *tenuifolia*, *Rorippa Nasturtium-aquaticum*: *microphylla*, *Parnassia palustris*: *obtusiflora*, *Saxifraga stellaris*: *foliolosa*, *S. nivalis*: *tenuis*, *Viola Riviniana*: *Reichenbachiana*, *Pimpinella Saxifraga*: *nigra*, *Oxycoccus palustris*: *microcarpus*, *Veronica longifolia*: *maritima*, *Artemisia borealis*: *bottnica*. Hence, if differences in chromosome number are observed between morphologically less distinct types previously described as species but not generally accepted, they should always be taken as a clear evidence of the correctness of regarding them as separate species.

Cytologists observing differences in chromosome number within some collective species are rendering little service to scientific taxonomy by reporting them only as new cases of "intraspecific polyploidy" and examples of lack of morphological characters of taxonomical value for separating the biologically isolated groups. Before publication they should always send good herbarium sheets to an

able taxonomist, if possible a specialist of the group in question, and ask for his help in determining the taxonomical status of the types. In most if not all cases the taxonomist is certainly able to tell the cytologist that his "intraspecific" types have previously been separated as species, or ought to be classified as such based on some major or minor morphological differences perhaps not observable at the first glance by an untrained eye.

Discussion

W. H. CAMP: Local observations are of little use in these situations. What is necessary is an understanding of the origin of the polyploid. There is little autopolyploidy; much is allopolyploidy. In several instances mentioned by Dr. LÖVE one ancestral diploid and the allotetraploid are in Europe; the allotetraploid and the other ancestral diploid are in America. Since the allotetraploids (as other polyploids) are segregative they will produce population segments superficially (and confusingly) similar to either ancestral diploid. These, however, are not part of the same biological populations and must be dealt with as separate systematic taxa of more than intraspecific rank. L.

N. W. SIMMONDS: We cannot assume isolation between plants of different ploidy because uneven polyploids are often appreciably fertile, especially if vegetative propagation permits a long life. This is likely to be true at all levels of ploidy but especially at the higher levels, where uneven ploidy in a hybrid ($5n$, $7n$) will have a smaller effect on fertility than the triploid. Thus isolation is likely to be incomplete, at least in autopolyploids, and introgression may occur.

CORNELIUS H. MULLER (Santa Barbara, Calif.)

Ecological Control of Hybridization in *Quercus*: A Factor in the Mechanism of Evolution

The ecological requirements of *Quercus* in Texas limit the contacts of several pairs of

genetically compatible species. Thus, *Quercus Havardi* on deep sand and *Q. Mohriana* on limestone come in close contact only where erosion of the sand plain exposes limestone. Although hybrids result freely from such contacts, they are confined strictly to areas of mixture of sand and limestone comprising habitats intermediate between those of the parents. Similarly, *Q. grisea* on igneous rock or dolomitic limestone comes in contact with *Q. Mohriana* commonly on dolomitic limestone and less commonly where igneous rock and limestone adjoin. In this instance a far greater exchange of characteristics occurs on dolomite than at the igneous contact, because dolomite is itself an intermediate habitat favorable to both species and to their hybrids.

When species differ in their requirements of some climatic factor, their contacts may vary in breadth with changing climates. *Quercus Havardi* ranges eastward from southeastern New Mexico on sand of varying depth and purity. *Quercus stellata* ranges westward onto the dry plains on sandy clay or clay overlaid by sand. Although these species overlap in range only sporadically in northern Texas and southwestern Oklahoma, their hybrids appear 100 to 200 miles west of the westernmost present occurrence of *Q. stellata*. During the pluvial period *Q. stellata* undoubtedly grew where its hybrids now grow.

These controls of hybridization played a decisive role in the speciation of *Q. Margaretta* and *Q. Drummondii*. During the pluvial period which carried *Q. stellata* westward, *Q. Gambelii* migrated from the Rocky Mountains eastward across the sandy zones of the Great Plains onto similar deep sand along the Gulf Coastal Plain. Because *Q. stellata* is excluded from deep sand, hybridization of this species with *Q. Gambelii* was strictly limited. Subsequent termination of the pluvial period eliminated *Q. Gambelii* from the Plains and thus isolated the two ends of the population, leaving prototypic *Q. Gambelii* in the Rocky Mountains and its derivatives on the Coastal Plain. The easternmost of the Coastal Plain

population, exhibiting little influence of *Q. stellata* hybridization, has undergone speciation as *Q. Margaretta*. However, at the westernmost extremity of the Coastal Plain population there occurs an area of much more common hybridization. Here there has developed an interbreeding population now stabilized as *Q. Drummondii* and showing much stronger gene flow from *Q. stellata*. Both *Q. Drummondii* and *Q. Margaretta* are surrounded by *Q. stellata* throughout their ranges, but hybridization is still being limited by their intolerance of one another's habitats.

D. H. VALENTINE (Durham) *Interspecific Compatibility and Hybrid Fertility as Taxonomic Criteria*

When pairs of allied diploid species are examined, a wide range of compatibility and hybrid fertility is to be found, from forms which are highly intercompatible and interfertile to forms which will not cross at all. In exploring the degree of relationship between diploid ecospecies (gradual-ecospecies) in which the hybrids show some degree of infertility, as many types of criteria as possible should be used, and in particular, weight should be given to compatibility, especially as it affects the formation and viability of hybrid embryo and endosperm. Work in progress on *Primula*, section *Vernales*, and *Viola*, section *Nominum*, illustrates this point.

In the *Primula* spp. under investigation (*P. vulgaris* HUDS., *P. elatior* SCHREB., *P. veris* L., etc., $n=11$) hybrid fertility is moderate or high, and pairing at meiosis in the hybrids is fairly complete; on the other hand, though the species are cross-compatible as regards pollen, they are highly incompatible with respect to the formation of embryo and endosperm. In all crosses, many of the embryos die or cease development at an early stage. This phenomenon is undoubtedly important in the isolation of the species, and also affords a criterion by which the extent to which they are geneti-

cally different may be estimated. It is thus useful taxonomically.

In the *Viola* spp. under investigation (*V. reichenbachiana* JORD., *V. rupestris* SCHMIDT, *V. stagnina* KRT., *V. mirabilis* L., etc., $n=10$), hybrid fertility is low (pairing at meiosis has not yet been determined); but when the species are crossed a better yield of good hybrid seed, with well-formed embryo and endosperm is generally obtained than in the *Primula* spp. Thus incompatibility leading to death of the embryo is here probably less important as an isolating factor than hybrid sterility.

It may be noted that the *Primula* spp. are self-incompatible and out-breeding, the *Viola* spp. self-compatible and to a considerable extent inbreeding. DARLINGTON and MATHER have suggested that in species which are habitual inbreeders, barriers preventing inter-specific hybridization are likely to be absent, and our observations are not inconsistent with this hypothesis. It may be concluded that the extent to which compatibility and hybrid fertility can be used as taxonomic criteria may vary with the breeding system of the group under investigation.

Discussion

H. G. BAKER: In *Armeria* very wide crosses are remarkably fertile, even intersectional crosses. Yet, apart from a number of races of *Armeria maritima*, all species appear to be obligatorily out-breeding. Species occur in conjunction particularly in the Iberian peninsula and putative natural intersectional hybrids are found.

M. SAKISAKA (Tokyo)

Critical Considerations of Chromosome Numbers in Relation to Plant Habit (Life Forms)¹

There are remarkable dissimilarities of plant habits between the plants with a small number

¹ Abstract of paper submitted but not read.

of chromosomes and those with a large number of chromosomes. In herbaceous plants, those with small numbers of chromosomes have a short life (annual habit) while those with large numbers of chromosomes have a long life (perennial habit). The two groups of plants differ from each other in fertility, activity, adaptability, rate of growth, and hybridity. The following are some of the examples; the first part shows small-number plants, the second part being large-number plants. The chromosome numbers are shown with the basic number in parenthesis.

Small number (diploid):

<i>Alopecurus aequalis</i>	14 (7)
<i>Bromus japonicus</i>	14 (7)
<i>Festuca Myuros</i>	14 (7)
<i>Sonchus oleraceus</i>	16 (8)
<i>Helianthus annuus</i>	34 (17)
<i>Solanum Melongena</i>	24 (12)
<i>Ipomoea Nil</i>	30 (15)
<i>Vicia sativa</i>	14 (7)
<i>Polygonum viscosum</i>	22 (11)

Large number (polyploid):

<i>Alopecurus pratensis</i>	28 (7)
<i>Bromus unioloides</i>	28 (7)
<i>Festuca rubra</i>	28 (7)
<i>Sonchus arvensis</i>	64 (8)
<i>Helianthus tuberosus</i>	102 (17)
<i>Solanum tuberosum</i>	48 (12)
<i>Ipomoea Batatas</i>	90 (15)
<i>Vicia unijuga</i>	28 (7)
<i>Polygonum filiforme</i>	44 (11)

There is gradual dominance of vegetative propagation (rhizome, tuber, bulb, bulbil, or runner) over seed propagation, from diploid to polyploid plants, in the same genus, as in the following examples (see next page): We can recognize that diploid plants propagate by seed, while polyploid plants become less

Diploid (no rhizome): Tetraploid (less rh.): Hexaploid (much rh.): Octoploid (extreme rh.):

<i>Chrysanthemum coronarium</i>	<i>C. indicum</i>	<i>C. morifolium</i>	<i>C. Decaisneanum</i>
<i>Polygonum orientale</i>	<i>P. japonicum</i>	<i>P. amphibium</i>	<i>P. Reynoutria</i>
<i>Dioscorea tokoro</i>	<i>D. japonica</i>	<i>D. sativa</i>	<i>D. bulbifera</i>

fertile and propagate vegetatively. The polyploid plants in different families show plant habit or life form such as life period or various life forms of vegetative propagation.

HERBERT LAMPRECHT (Landskrona)

*Taxonomy on Genic and Cytological Basis*¹

Taxonomy was hitherto mainly based on the study of morphological and physiological characters. Besides, the geographical distribution has played an important part. Since about 25 years taxonomic investigations were also made on a cytological basis. In a number of cases speciation could be artificially repeated by a doubling of the genom or by the addition of genomes of different species.

However, in all these cases no qualitatively new characters were arising. As the development of qualitative characters always seems to be caused by differences in genes, taxonomic studies on a gen-analytical basis seem now to be of the greatest interest. The study of the species cross *Phaseolus vulgaris* × *coccineus* and *vice versa* has demonstrated that a single gene can cause an insurmountable barrier between two species. As one allele of such a gene is characteristic of one species, the other of another species, these genes were called interspecific genes. When artificially transmitted to another species, the allele of an interspecific gene causes sterility or lethality and thus the species barrier.

R. RUGGLES GATES (Cambridge, Mass.)

The Taxonomic Units in Relation to Cyto-Genetics and Gen-Ecology

The search for an inclusive definition of species, which would apply to bacteria, Cya-

nophyceae and mammals, is vain and should be given up. New inheritable forms can arise in a multitude of ways, as shown by the work in cytogenetics and experimental ecology. One school of geneticists have attempted to erect reproductive isolation as the criterion of species. They describe "new species" of *Drosophila* where there is virtual lack of morphological differences. This is a contradiction in terms, because taxonomy is founded on the recognition of inherited phenotypic differences. Intersterility can arise at any stage in the process of speciation. It may be the first stage or the last or anywhere in between. Cases are cited in illustration. The development of intersterility between contemporary species of a genus is incidental and may not occur at all. Time is a fourth dimension in the concept of species, and when one species gives rise to another in geological time there has obviously been continuous breeding from the mother to the daughter species.

In speciation there are two main streams of change, (a) gene mutations, which alter the phenotype, (b) chromosome changes, such as translocations, which alter gene linkages and introduce intersterility. Both types of change are subject to natural selection, and individuals heterozygous for a translocation may show more vigour in certain conditions. A species is a dynamic system consisting of successive populations of individuals. Much evolution, but by no means all, has occurred at the diploid level.

In a discussion of subspecific units, the work of CLAUSEN, KECK and HISEY is cited, with ecotypes and transplant experiments in the genera *Achillea* and *Potentilla*; also the nature of species in *Antirrhinum*, *Silene*, *Platanus*, *Crepis*, *Zauschneria*, *Balsamorhiza*, *Catalpa*, *Quercus*, *Pinus*, *Parthenium*, *Solidago*, *Lactuca* and other genera.

¹ Abstract of paper submitted but not read.

The taxonomist recognizes that there are well defined species and species which the taxonomist must define by "drawing a line somewhere." The lumpers and splitters play reciprocally useful rôles in taxonomy, the former emphasizing the resemblances, the latter the differences, between related forms.

Discussion

R. E. CLELAND: Dr. GATES has stated that there are more than 70 species in the subgenus *Euoenothera* of the genus *Oenothera*. On the basis of work being done jointly by Dr. P. A. MUNZ and our group, it seems probable that the number of species which MUNZ will recognize will be many fewer than this—perhaps not over a dozen. The *Euoenothera* population consists of hundreds, if not thousands, of individual lines, breeding true because of large circles and balanced lethals, and fairly effectively isolated from each other by their self pollinating habit. Many of GATES' species are merely random selections from among these lines. Our work shows that these innumerable isolated lines fall rather neatly into groups, of which we have been able to recognize only 7 or possibly 8 up to the present time. These groups possess in most cases sufficient phenotypic distinctness to be

useful taxonomically. Each group occupies a distinct geographical area, and the RENNERS complexes in each group have distinctive arrangements of the end segments. The fact that the alpha or egg complexes, for instance, in a given group of races, have similar or identical segmental arrangements is evidence that they are phylogenetically related. There seem to be in the North American *Euoenotheras* seven or eight distinct groups of races, each representing the present end-point of a separate line of evolutionary development. I am inclined to consider these as species in spite of the fact that the self pollinating habit prevents easy distribution of genes throughout such species. I am leaving the naming of species in this genus to MUNZ, and do not know what he will finally do with this material.

D. D. KECK: Sterility barriers are correctly described by Dr. GATES as insufficient criterion for "what is a species." The experimental taxonomist obtains the data from a more objective classification. He must use numerous criteria and apply common sense. A classification based on experiment often does not end up very unlike a classification made by a competent taxonomist, except that the changes made are founded on more complete data. The competent taxonomist has been using morphological-distributional differences that usually mark the natural units.

SESSION 8

Jointly with Sections CYT and GEN: July 20th, 9 a. m.—1 p. m., See page 219

FOREST BOTANY, FOB

President: D. V. BAXTER

*Vice-Presidents: W. BAVENDAMM, N. F. BUCHWALD, E. EIDE,
H. GAUSSEN, V. KUJALA, E. MORK, A. PAVARI, M. H. STEVEN, C. SYRACH-LARSEN,
R. TÜXEN, H. VAN VLOTEN, W. VON WETTSTEIN*

Recorder: E. BJÖRKMAN

Vice-Recorder: O. LANGLET

SESSION 1

July 12th, 1—5 p.m., Attendance: 42 members

Chairman: D. V. BAXTER, Recorder: E. BJÖRKMAN

SUBJECT:

Forest Types

D. V. BAXTER (Ann Arbor, Mich.)

Opening Remarks

Till mina vänner, kolleger, botanister och skogsvetenskapsmän från hela världen!

Det är mig en stor ära att som president för FOB-sektionen få välkomna Eder till Sverige och till den Sjunde Internationella Botanistkongressen. Vi som äro gäster från fjärran delar av världen känna väl till att våra svenska kolleger ha lämnat många av världens stora bidrag till skogsbotaniken.

Arbeten som man har utfört i skogen och på laboratoriet i Linné's och Fries' hemland ha varit en inspiration för oss alla. Jag värderar forskare som Prof. Dr. ELIAS MELIN, Prof. Dr. TORSTEN LAGERBERG, Prof. Dr. ERIK BJÖRKMAN, Dr. ERIK RENNERFELT och de många andra svenska vetenskapsmännen. Jag vill särskilt tacka Prof. BJÖRKMAN för det utomordentliga arbete han har gjort för FOB-sektionen.

Jag är mycket glad över att vi kunde mötas i Sverige, och jag hoppas, att er vistelse här blir både givande och trevlig.

English translation:

To my friends, colleagues, botanists and forest scientists from the whole world:

It is a great honour for me as president of Section FOB to welcome you to Sweden and to the Seventh International Botanical Congress. We who are guests from far away parts of the globe know well that our Swedish colleagues have made many of the most important contributions in the field of Forest Botany.

The work that has been done in the forests and in the laboratories in the home country of Linné and Fries has been an inspiration to all of us. I greatly value the eminent work of such investigators as Prof. Dr. ELIAS MELIN, Prof. Dr. TORSTEN LAGERBERG, Prof. Dr. ERIK BJÖRKMAN, Dr. RENNERFELT and many other Swedish scholars. I want to thank Prof. Dr. BJÖRKMAN

especially for the magnificent work that he has done for the FOB Section.

I am very glad we have been able to meet here in Sweden, and I hope that your stay here will be both pleasant and profitable for you.

H. GAUSSEN (Toulouse)

Les forêts des Pyrénées françaises

Les Pyrénées ont seules en Europe, le privilège de posséder une flore contenant des éléments mésogéens, atlantiques, médioeuropéens et arcticoglaciacaires. Cela leur confère une grande richesse de flore herbacée.

Pour les arbres, le climat actuel convient à beaucoup d'arbres de pays froids qui d'origine centreuropéenne ou septentrionale ont progressé vers le S. W. lors des glaciations.

Certains ne paraissent pas avoir eu un temps suffisant pour arriver aux Pyrénées, citons: *Picea excelsa*, *Larix europaea*, *Pinus Cembra*, *Pinus Mughus*, *Pinus Pumilio*, *Ostrya carpinifolia*, *Quercus Cerris*.

Par contre, dès le Tertiaire, *Pinus uncinata*, *Pinus Salzmanni*, *Quercus Tozza*, étaient installés aux Pyrénées.

La diversité écologique aux Pyrénées est extraordinaire. On peut dire que tous les types européens sont représentés. La gamme géologique est à peu près complète avec de multiples faciès.

Tout cela donne à la forêt pyrénéenne une assez grande diversité malgré le nombre restreint des espèces forestières.

En partant de la Méditerranée, on peut citer les étages:

Euméditerranéens à Myrte, Pin Pignon, Olivier, Chêne-liège, Pin mésogéen, Chêne vert.

Notons l'absence du Pin d'Alep, du Cyprès qui réussissent fort bien quand on les introduit.

Subméditerranéens: à Pin de Salzmann, Chêne pubescent, Chêne vert.

Collinéens: à Chêne pubescent avec chêne sessile au fond des vallées.

Montagnards secs à Pin sylvestre, humides à Hêtre et Sapin.

Subalpin à Pin à crochet et Bouleau.

En partant de l'Atlantique on peut citer les étages:

Atlantiques: à Pin maritime, Chêne-Liège, Chêne Pédonculé, Chêne Tauzin.

Collinéen: à Chênes Tauzin, pédonculé, sessile.

Montagnard: à Hêtre et Sapin.

Subalpin: à Pin à crochets.

Le Sapin ne dépasse pas à l'W. la forêt d'Irati, le Pin à crochets le Pic d'Orhy. Le Chêne tauzin ne dépasse pas à l'E. la vallée de la Garonne.

En partant de la plaine centrale il faut, dans l'étage collinéen, souligner l'importance des arbres ripicoles: Aunes, Peupliers, Saules et Frênes, Tilleul et la faible pénétration du Charme.

Quelques curiosités de répartition méritent d'être signalées: Reliques glaciaires, (*Pinus uncinata* à 800 m. d'altitude, Sapinière de Ste Croix Montbrun). Reliques xerothermiques (*Quercus Ilex*, *Juniperus thurifera*, *J. macrocarpa*, Hybride, *Q. Ilex* × *coccifera*, *Phillyrea angustifolia*). Passage du Pin sylvestre d'Espagne par les cols inférieurs à 2400 m d'altitude.

La dépopulation considérable qui a bien réduit l'encombrement par les troupeaux, un climat favorable, font de l'étage montagnard des Pyrénées centrales un terrain de choix pour réaliser en grand l'introduction d'exotiques. La création d'arboretums et d'un « silvetum » auprès du Laboratoire de Jouéou à Luchon répond à ce but.

Discussion

F. FLORSCHÜTZ: Je serais heureux de savoir si l'on sait déjà quelque chose de l'histoire forestière des Pyrénées pendant les périodes Holocène et Pléistocène.

H. GAUSSEN: Au sujet de la flore forestière de la fin du Tertiaire il y a eu des travaux de Rerolle sur la Cerdagne (Pyrénées Orientales) qui montrent que *Pinus uncinata*, *Abies pectinata* et *Fagus sylvatica* existaient en montagne à ce moment là.

R. TÜXEN (Stolzenau/Ws.)

Über den Stand der forstlich-soziologischen Kartierung in Deutschland

Die deutsche Forstwirtschaft hat ungewöhnliche Aufforstungen vorzunehmen und muss dafür alle zugänglichen Planungs-Unterlagen zu erlangen suchen. Unter ihnen steht die Vegetationskartierung an erster Stelle, die allerdings erst zögernd benutzt wird. Ausser einzelnen Revierverwaltern beginnen erst wenige höhere Verwaltungen den unschätzbaren Wert pflanzensoziologischer Karten für die Forstwirtschaft voll zu erkennen.

Wertvoller als Übersichtskarten kleiner Massstäbe (HUECK: Deutschland, KNAPP: S-Hessen und N-Baden, MEUSEL: Mittel-Deutschland, OBERDORFER: Baden, TÜXEN: Krs. Gronau, NW-Deutschland) sind für die Wirtschaft Karten grossen Maßstabes. Bis zum Kriege lagen von wenigen Messtischblättern (1:25000) in O-Deutschland (HUECK), Württemberg (FABER, SCHLENKER), Baden (OBERDORFER) und von einem geschlossenen Gebiet aus Niedersachsen mit etwa 200 Messtischblättern (TÜXEN und Mitarbeiter) soziologische Waldkarten vor, in denen (mit einigen Ausnahmen) ohne Rücksicht auf die heutigen forstlichen Kunstbestände die natürlichen Waldgesellschaften eingetragen waren, wie sie erkannt werden aus Relikten, Kontakten, Bodenprofil, Forstgeschichte usw.

Nach dem Kriege wurden vor allem von der Zentralstelle für Vegetationskartierung (ZfV) in allen Teilen W-Deutschlands, am planvollsten im Landesteil Braunschweig, zahlreiche Forstämter und -Güter im Maßstabe 1:10 000 kartiert. Die Karte der Eilenriede bei Hannover von LOHMEYER und ELLENBERG ist veröffentlicht. In S-Baden kartierte OBERDORFER in gleicher Weise. (Eine Übersichtskarte von Hessen wurde nach anderen Gesichtspunkten von KNAPP hergestellt.)

Die ZfV arbeitet jetzt nach folgender Methode: Für jedes zu kartierende Gebiet werden soziologische Aufnahmen und Tabellen, forstliche Charakteristik, Bodenprofile und allgemeine Ökologie der erkannten Gesellschaften

neu bearbeitet. Dann erst beginnt die Kartierung der noch vorhandenen Reste natürlicher Wald- und der künstlich begründeten Forstgesellschaften. Diese werden nach den herrschenden Holzarten zusammengefasst und durch Differentialarten gegliedert. Sie können damit wie bisher leicht auf die „natürlichen“ Waldgesellschaften zurückgeführt werden. Dadurch werden alle örtlichen Besonderheiten deutlich erfasst, ohne dass für die Generalisierung Schwierigkeiten entstehen. Bei der Durchführung der Kartierung im Gelände leistet ein von der ZfV erprobtes Verfahren zur Auswertung von Luftbildern besondere Dienste.

Der Wirtschaftler braucht leicht lesbare Karten. Darum können nicht in einem Bezirk, der nur einen Verband oder gar nur eine Assoziation enthält, alle auszeichnenden Unterheiten in einer einzigen allgemein festgesetzten Farbe, nur durch Signaturen unterschieden, dargestellt werden. Vielmehr werden für jede Karte grössten Maßstabes jeweils alle Farbmöglichkeiten voll ausgenutzt. Der Nachteil dieser Farbwahl, dass ein Revierverwalter eine fremde Karte nicht sofort lesen kann, ist unerheblich, weil er dazu kaum in die Lage kommt und sich in diesem Falle der Legende der neuen Karte bedienen kann.

Auch bei der Herstellung von Vegetationskarten für andere Wirtschaftszweige (Grünland- und Wasserwirtschaft, Strassen- und Wasserbau usw.) werden ebenfalls alle Farbmöglichkeiten verwendet. Für Übersichtskarten kleineren Maßstabes (z. B. Naturlandschaftskarten) bleiben einheitliche Standardfarben jedoch erstrebenswert.

Systematisch einander nahestehende Gesellschaften werden ähnlich gefärbt und signiert. In unseren Karten bezeichnen blaue Töne im allgemeinen die auf feuchten, rote dagegen die auf trockenen Standorten lebenden Pflanzengesellschaften.

Jeder Karte wird ausser einem ausführlichen Text eine kurze synoptische Auswerte-Tabelle beigegeben, welche Namen, Kennzeichnung und örtliche Verbreitung der in der Karte ausgedehnten Gesellschaften, die Beschreibung

ihrer Standorte und endlich für jede Angaben über natürliche Pionier- und Wirtschafts-Holzarten und standortsgemässe zusätzliche fremde Wirtschafts-Holzarten nach Art und Menge sowie für Sträucher der Waldmäntel und andere Erläuterungen enthält.

Discussion

H. GAUSSEN: Quels principes avez-vous suivis pour établir les colorations des cartes? Avez-vous eu un but écologique dans leur emploi?

F. FLORSCHÜTZ: Ich möchte gern wissen, ob Dr. TÜXEN der Meinung ist, dass *Pinus* während des Holozäns in NW-Deutschland ausgestorben ist.

T. HÅKANSSON: Professor TÜXEN erwähnte, dass *Querceto roboris-Betuletum* in Deutschland die ärmsten Böden besiedelt; *Querceto sessiliflorae-Betuletum* dagegen käme auf reicheren, forstlich produktiveren Böden vor. Dies scheint mir im Widerspruch zu den Befunden in Schweden von Professor WEIMARCK in Lund zu stehen. Dieser hat durch Experimente und Beobachtungen im Felde erwiesen, dass *Quercus sessiliflora* auf saureren, ärmeren und forstlich weniger produktiven Böden sehr gut gedeiht. Sie scheint daher *Q. Robur* auf solchen Böden in Südwest-Schweden zu verdrängen.

R. TÜXEN: Auf die Frage von Professor GAUSSEN, ob bei der Farbgebung auch die Eigenschaften des Standortes berücksichtigt werden, antworte ich, dass Gesellschaften feuchter Böden mit blauen, solche trockener Böden mit roten Farben dargestellt werden. — Professor FLORSCHÜTZ fragt nach dem Vorkommen spontaner Kiefern in NW-Deutschland. Ich halte nach den pollenanalytischen Feststellungen für möglich, dass die wenigen Kiefern, die in NW-Deutschland die Nach-Kiefernzeit überdauert haben, auf Binnendünen oder auf Hochmooren gelebt haben. Sie sind heute nicht mehr aufzufinden, nachdem der künstliche Anbau der Kiefer so ungeheure Ausmasse angenommen hat. — Dr. HÅKANSSON glaubt, meine Befunde über die Standorte von Stiel- und Traubeneichen-Birkenwald stehen mit denen

von WEIMARCK in Schonen im Widerspruch. Ich weise darauf hin, dass in Schonen aber das *Querceto roboris-Betuletum*, eine endemische Gesellschaft NW-Deutschlands und Hollands, garnicht vorkommt, und dass dort infolgedessen — übereinstimmend mit WEIMARCKS Auffassung — das *Querceto sessiliflorae-Betuletum* die ärmsten Böden besiedelt.

V. KUJALA (Helsingfors)

On the Geographical Distribution of Forest Types

It is possible to limit natural plant communities and to classify them more narrowly or more widely according to different methods. From the forest point of view it is necessary also to consider the largest plants, the trees, as regular members of plant communities—therefore a wider plant community area is inevitable, not only because of the trees. Often the smaller plants, belonging to the ground vegetation, occur in groups. Some of these plants propagate chiefly by means of seeds. The seeds usually fall in the neighbourhood of the mother plant, with group occurrence as a consequence.

Some other species propagate vegetatively by means of their rhizomes, and therefore occur in large but confined areas. Furthermore, some species thrive particularly well around the trees. Thus the trees cause further inequality or inhomogeneity in the plant cover. Homogeneity in occurrence is not at all a common characteristic of forest plants. It is obvious that the forest plant communities and the sample plots must not be too small, if we wish to allow the plants adequate space in order to reveal the sociologic regularities in the occurrence and distribution of the plants. These plots should be at least 1/10th of a hectare.

Another noticeable point is the varying stability of different plant communities. In the forests there are evidently very steady climax-communities, and others which are constantly changing. These last-mentioned types of community are mostly caused by some

sudden but potent factor. It is obvious that the relatively permanent climax-communities are in general of far greater significance in Nature than temporary ones, especially if we think of ancient times, when the influence of Man upon Nature was not yet so widespread and so considerable.

In view of these facts the forest type system of A. K. CAJANDER seems very important, and is of great international significance, since it affords an exact basis for estimating the possibilities of growing different tree species at different sites in different countries and for the exchange of experience gained in forest science and practice.

In Finland, proceeding from South to North, we find that the forest types change continually with the climate. In northern Finland we find no southern type—but we do find more or less corresponding parallel types or sub-types. Sometimes a northern type is at first sight very like a southern one, but on closer examination we find differences in all layers of the plant cover.

Also in countries south of Finland, in the Baltic States, in Poland, in the mountains of Czechoslovakia and Hungary, taking forest types in general, the same types occur over wide areas and also under different climatic conditions. Closer examination reveals, however, that changes in the species are effected by the climate.

It is evident that if we wish to explain all these different climatic forms of forest vegetation types, in order to satisfy completely forestry demands, the examination must be very precise and not too restricted with regard to material.

Some parts of Canada with a climate almost corresponding to that of Finland, have forest vegetation types parallel to the Finnish ones. There are, unfortunately, no areas where the climate is exactly the same as in Finland—the difference in geographical latitude alone makes this impossible. However, where the climatic conditions are almost the same, all forest vegetation types correspond to those in Finland. We

do not find any entirely unique Canadian types in such regions.

It would probably be possible to establish corresponding forest types everywhere in the northern coniferous region where the climate is more or less the same. It affords a common ground to forest—and also to many ecological—investigations in general.

C. REGEL (Zürich)

Ist der Wald eine Landschaft oder ein Pflanzenverein?

Unter Landschaft verstehen wir ein Stück der Erdoberfläche, das aus Boden, Gewässern, Lufthülle, Vegetation, Tierwelt, Mensch und Menschenwerk besteht und deren Zusammenwirken eine Einheit im Sinne eines Wirkungszusammenhanges darstellt. Sie umfasst die Gesellschaften der Organismen (Biocoenosen), d. h. von Pflanzen (Phytocoenosen), von Tieren (Zoocoenosen) und von Menschen (Anthropocoenosen), andererseits die Komplexe der anorganischen Erscheinungen der Erdrinde, des Wassers und des Klimas. Der Wald ist als Landschaft aufzufassen, die Waldtypen CAJANDERS, KRÜDENERs, SUKATSCHEWs, REGELs (auf Kola) u. a. sind Landschaften, nicht Pflanzenvereine, da zu ihrer Charakteristik nicht die Pflanzendecke allein, sondern auch andere Merkmale, wie Boden und Klima benutzt werden. Der Wald ist eine soziale und eine geographische Erscheinung, sagt MOROZOW, und nach SUKATSCHEW ist der Wald eine Geocoenose und die Waldassoziation die rein botanische Klassifikationseinheit der Vegetationsdecke. Der Wald ist ein Landschaftstyp, wie Tundra, Steppe, Moor, Wüste, Wiese u. s. w., in dem die Bäume oder auch bestimmte aus Bäumen bestehende Vereine vorherrschen, von denen er daher seinen Namen hat. Die Pflanzensoziologische (oder -coenologische) Benennung des im Walde vorherrschenden Pflanzenvereines wäre Lignosa, Gehölz oder Waldverein oder Waldgesellschaft. Die Klassifikation des Waldes als Landschaft kann nur auf Grund sämtlicher Merkmale erfolgen, eine Klassifikation

auf Grund eines einzigen Merkmales wäre eine künstliche und nicht natürliche. Der Wald als Pflanzenverein ist aus verschiedenen Assoziationen zusammengesetzt, die wir als Einheiten der Mehrschichtassoziationen auffassen, und aus Unionen, die Einheiten des Einschichtvereines, der Synusie, sind. Eine Klassifikation der Waldvereine kann nur auf Grund von botanischen Merkmalen erfolgen, wie floristische Zusammensetzung, sozialer Aufbau, Deckungsgrad, Abundanz, Florenelemente, Treue u.s.w.,

und nur durch Berücksichtigung mehrerer solcher Merkmale, nicht eines einzelnen allein, ist eine natürliche Klassifikation möglich. Als Landschaft betrachtet ist der Wald eine Realität, auch kann man sich die Waldlandschaft als Abstraktion vorstellen. Als Pflanzenverein ist der Wald jedoch eine Abstraktion. Für das entsprechende konkrete Gebilde, d. h. die botanische Charakteristik ohne die Merkmale der Umwelt, die schon zur Landschaft gehören, besteht weder Name noch Vorstellung.

SESSION 2

Jointly with Section PHP: July 17th, 9 a.m. — 1 p.m., Attendance: 90 members

Chairman: D. V. BAXTER, Recorder: E. BJÖRKMAN

SUBJECT:

Attacks by Fungi on Forest Trees

G. F. GRAVATT (Beltsville, Md.) *The Problem of World-Wide Spread of Forest Diseases*

The continued spread of forest tree diseases from continent to continent is a steadily increasing menace to the productivity of all forests. It is forecast that five major introduced diseases now established in the United States will ultimately affect forest production and species composition on perhaps 170 million acres. In many countries the forest tree diseases have not been studied. Even in those countries where forest pathology is well advanced, it is often impossible to determine whether a disease is native or introduced. Once an introduced forest disease becomes widely established, it is a perennial problem. Probably 500 years hence in America white pine blister rust and the chestnut blight will still be problems.

Forecasting the probable increase in number and the effect of imported diseases on world forests 100 or 200 years hence has a large element of guess work. However, forecasting is necessary to make people realize how critical the situation can become. The present and the

probable future status of introduced forest diseases are serious enough to justify an immediate and thorough reexamination of all aspects of the problem.

Discussion

D. V. BAXTER: We have heard about many diseases in American forests from Mr. GRAVATT. The oak wilt is reported in this paper from a number of American localities. European forest pathologists will be interested in knowing where the fungus involved came from. Is it possible to know where such a fungus originated?

G. F. GRAVATT: It is not known where the oak wilt fungus originated.

D. MULDER: 1. Are there any deficiency diseases known of forest trees?—2. Is there any relation between the nutritional condition of forest trees and the parasitic diseases described by Mr. GRAVATT?

G. F. GRAVATT: 1. I do not remember any deficiency disease of undisturbed forest trees in the United States. There is a zinc deficiency disease in cultivated pecans and this same trouble shows up in the wild pecans when the

wild stand is thinned and cultivated. It does not show up in undisturbed wild pecans. We have an iron deficiency particularly of oak on ornamental and street trees.—2. Nutritional conditions of forest trees in relation to diseases has not been adequately studied.

P. H. GREGORY: In discussing the new disease of sycamore maple, *Acer pseudoplatanus*, found in London, England, Dr. GRAVATT drew attention to its resemblance to an American disease of persimmon. Could he give any information on the host range of the persimmon fungus? Professor T. S. SADASIVAN has drawn my attention to another tree disease with strikingly similar symptoms, that on *Casuarina* in India caused by *Trichosporium vesiculosum* BUTLER. The English sycamore disease appears menacing, and it is natural to assume that it is a recent importation.

G. F. GRAVATT: In reply to Professor GREGORY's question as to the host range of the persimmon wilt fungus, *Cephalosporium diospyri*, it is prevalent on our American persimmon, *Diospyros virginiana*, and was found in one case on *D. kaki*. Both *D. kaki* and *D. lotus* are highly resistant, but the fungus can be carried in their tissues. By inoculation, *D. texana* and *D. ebenaster* are known to be susceptible.

L. HUTCHINS (Beltsville, Md.)

On Virus Diseases of Forest Trees

One of the least explored fields of forest pathology is that of virus diseases. The present paper does not review the world literature, but examples are cited to show that a wide range of forest tree species is susceptible. Special emphasis is given to virus diseases of forest trees in the United States of America.

Discussion

D. V. BAXTER: Many new diseases of unknown cause are now appearing in American forests. Dr. HUTCHINS stressed the necessity of making observations and tests for a virus as well as for fungi when making determinations

of the agent responsible for the condition. Grafting techniques were described. It will be of interest to hear about the success, Dr. HUTCHINS, the Division of Forest Pathology has attained in your experiments with grafts of *Pinus echinata*. These pertain to the search for the cause of the "little leaf" disease of short leaf pine.

L. HUTCHINS: "Little leaf" disease of pine has not been transmitted by graft inoculation in experiments thus far performed. Many bark grafts from diseased to healthy short leaf pines were made several years ago and are still living, but they have not transmitted the disease. Scion grafts from diseased to healthy trees do not survive in a great many cases, but those that were successful have not transmitted "little leaf" disease. Similarly, approach grafts between roots of diseased trees and healthy trees have given no positive transmission of the disease.

J. C. WENT: 1. What are the symptoms of the zonate canker of elms? Does it show in the leaves?—2. For how long time are the two resistant numbers of American elm tested on their resistance to the Dutch elm disease?

L. HUTCHINS: 1. The symptoms of zonate canker on the branches are a target type canker with definite concentric rings showing on the bark and on the surface of the wood beneath the bark. Canker may develop at the base of green shoots which have died from the effects of the disease. Cankers may enlarge and girdle the stem, which then dies. The leaves soon after they come out in the spring develop small necrotic areas. Succulent lateral sprouts commonly bear necrotic spotted leaves.—2. The two American elms which have been selected for resistance to Dutch elm disease have been under test for approximately 10 years. They were inoculated each year for 3 successive years, and then again 2 years later. In 1950 a mixture of 50 strains of the Dutch elm fungus was used in making inoculations. Both of the previously resistant elms developed severe symptoms of the disease following inoculation in 1950.

N. F. BUCHWALD: 1. Dr. HUTCHINS told us that the virus is always confined to the roots

and to the wood of the affected trees. Do you not find the virus in the leaves?—2. Have you used serological methods to identify the viruses?

L. HUTCHINS: 1. I think here Dr. BUCHWALD refers to my discussion of phony peach disease, in which the virus appears to be confined to the woody cylinder. The disease is transmissible only by grafting, not by injections of expressed juice. Bark grafts alone do not transmit the virus to healthy plants, but inoculum consisting of infected wood with bark attached, so that callous can form and growth union can take place, does transmit the virus. Presumably a bridge of new wood is laid down which connects the wood of the inoculum with that of the healthy tree, and the virus passes through this bridge. The virus in many cases is confined to the roots, but the shoot wood sometimes is invaded, also.—Presence of the virus in the leaves is doubtful and has not been investigated, since the shoot may or may not be invaded and since transmission has been secured only with graft-inoculum containing infected wood.—2. Serological methods have not been employed because the juice expressed from diseased trees is not infective.

N. F. BUCHWALD (Köbenhavn)
Pseudotsuga and Phaeocryptopus
Gäumanni in Denmark

Phaeocryptopus Gäumanni was first noticed in Denmark (Jutland) in 1938. From that year the situation became critical for the cultivation of the Douglas fir in Denmark. The fungus spread rapidly in the following years. In 1948 the number of affected localities reached 70; and it is expected that within ten years all Danish stands of Douglas fir will become more or less infected by the fungus.

It has not been clearly explained to what extent *Ph. Gäumanni* causes the fall of the fir needles. Danish observers have often found infected needles which have been growing 4 or 5 years on the tree. The facts are, however, often obscured by the influence of external factors.

In the winter of 1946–47 the long period of severe black frost caused a considerable fall of needles in all Douglas stands. A thorough investigation was started in the summer of 1947 as to whether this needle cast was due to the severe winter alone or to the severe winter combined with the activity of *Ph. Gäumanni*.

In the winter of 1946–47 there was both a prolonged period of hard frost and a marked period of drought (October 1946–June 1947) together with a dry easterly wind most of the time.

A close investigation of 12 cultivation experiments with Douglas firs showed that these could be divided into two sharply distinguished groups. While freezing of terminal shoots occurred each time, needle shedding was only observed in 7 experiments, in which the Douglas firs were more or less seriously infected with *Ph. Gäumanni*. It was further shown that the needle shedding was fairly proportional to the intensity of the fungal attack, in so far as the plots which were most attacked showed the greatest fall of needles.

Thus everything seems to indicate that only the needles infected with *Ph. Gäumanni* were shed during and after the winter of 1946–47. It does not seem likely that the needles weakened by the fungus, were killed by the low temperature. It is far more probable that the death of the needles is due to desiccation. The bare ground was frozen to great depths and the roots of the trees were therefore unable to absorb water. This fact together with the prolonged drought and the prevailing easterly winds no doubt caused death by the desiccation of the infected needles.

The cause of the great fall of needles must therefore be attributed to the shedding of needles due to the severe frost together with a desiccation of the needles already weakened by the attack of the fungus. *Phaeocryptopus Gäumanni* must thus be considered the primary cause of the shedding.

All provenances of the green variety (var. *viridis*) seem to be very susceptible, but their resistance appears to differ. Unfortunately our

information on the provenances is deficient, and it is therefore difficult to say anything with absolute certainty. Everything would seem to indicate, however, that the Douglas firs from the Olympic National Forest around Louella in Washington are the most resistant trees, and that on the whole the provenances from Western Washington are the most suitable ones for Denmark.

It is as yet difficult to give a satisfactory answer to the important question why the Douglas fir is so much more susceptible to attack in Denmark and in Europe in general than in North America. The most obvious assumption is that when the Douglas fir is transferred to other climatic conditions, it loses its natural biological balance, in other words it becomes more susceptible in a different environment. But it is not certain that the susceptibility of the Douglas fir as determined by the environmental conditions is the only decisive factor. It is also conceivable that the environmentally determined virulence of the fungus plays a part too, in other words that the fungus develops better in Europe than in its native country. Finally, it must not be overlooked that we do not yet know anything about the physiological specialisation of the fungus, that is, whether different pathogenic races of the fungus exist.

Discussion

D. V. BAXTER: We have heard that certain forms of *Pseudotsuga taxifolia* are more resistant than others to this disease described so well by Dr. BUCHWALD. Is it possible, Dr. BUCHWALD, that a) trees grown under unfavourable conditions or b) trees naturally susceptible favour the development of the fungus so that a large fungus population appears—and because of this large population, more infection results even in moderately resistant forms?

N. F. BUCHWALD: In Denmark we always find that the Douglas fir trees grown under favourable conditions are infected, and we are inclined to consider *Phaeocryptopus Gämmani* a primary parasite.

H. VAN VLOTEN: Out of a number of Douglas firs of Dutch origin (taken from an old stand) sent to Württemberg in 1939 only 2 per cent were a little less heavily infected. Here may lie a chance for tree breeding.—The different lectures (GRAVATT, HUTCHINS and BUCHWALD) give clear evidence that a closer international cooperation is indispensable. As the only representative of the Board, I would therefore like to draw the attention of this meeting to the International Union of Forest Research Organizations. At a meeting in Helsinki one year ago, we decided to divide our forest research work into 11 different sections. One of these sections is number 24 on Forest Protection which I invite all forest pathologists to join.

N. F. BUCHWALD: In Denmark we have for many years noticed the same occurrence as that mentioned by Dr. VAN VLOTEN, that is to say that some individual trees in severely affected stands sometimes escape the attack. We would therefore recommend making a vegetative propagation of such especially resistant trees.

MILDRED K. NOBLES (Ottawa)

Cultural Identification of Fungi Causing Decay in Coniferous Trees of British Columbia

Decay studies on eight species of coniferous trees in British Columbia, Canada, have included the determination of the causal organisms by cultural methods. Identifications are made by comparing the physiological and morphological characters exhibited by the cultures when grown on malt agar and on malt agar to which gallic or tannic acid has been added with those of named cultures grown under the same conditions. To facilitate the comparisons a numerical key has been prepared.

The hosts studied were *Abies amabilis*, *A. lasiocarpa*, *Picea glauca*, *P. sitchensis*, *Pinus monticola*, *Pseudotsuga taxifolia*, *Thuja plicata*, and *Tsuga heterophylla*. Of the cultures isolated from decays 1825 or about 85 per cent of the

total have been identified as belonging to 60 species of Hymenomycetes, with 82 per cent of the isolates belonging to only 20 species and the largest numbers of isolates belonging to *Fomes pinicola*, *Polyporus Schweinitzii*, and *Stereum sanguinolentum*. Cultures of the majority of the species involved are readily identifiable and as a result more accurate information about a number of rots has been obtained. For example, a type of decay in *Abies lasiocarpa* and *Tsuga heterophylla* in interior British Columbia (formerly attributed to *Echinodontium tinctorium*) yielded cultures about half of which were *Echinodontium tinctorium*, half *Stereum sanguinolentum* not previously known to be important in these hosts. A white rot in *Abies lasiocarpa*, *Picea glauca*, and other conifers, previously all referred to *Poria subacida*, yielded cultures of two types similar except for the occurrence of characteristic oil-filled hyphae in one group. These latter were found to be isolates of *Corticium galactinum* which was thus demonstrated to be the cause of a decay easily confused with that caused by *Poria subacida*. The occurrence in *Polyporus tomentosus* var. *circinatus* of typical chlamydospores distinguishable from the chlamydospore-like swellings in *Polyporus tomentosus* permits the separation of cultures of these species and the similar rots caused by them. Differences in the cystidia in cultures of *Polyporus abietinus* and *Odontia bicolor*, alike in other characters, has made possible the separation of the cultures and the demonstration of *O. bicolor* as an important cause of decay in *Picea glauca* and other hosts. Cultures of *Trametes serialis*, *T. variiformis*, and *T. heteromorphus* are not separable on the basis of characters used in the key and for the separation of isolates of species in this group single spore cultures must be isolated and interfertility tests carried out.

H. ZYCHA (Hann. Münden)

Die Rindenfäule der Buche (*Fagus silvatica*)

Seit einer Reihe von Jahren vermehren sich die Hinweise auf ein Absterben älterer Buchen

(*Fagus silvatica*), das seinen Ausgang nimmt von charakteristischen Nekrosen in der Rinde des Stammes. Dieser von EHRlich (1934) als „Beech bark disease“, von mir als „Rindenfäule“ bezeichneten Erkrankung folgt eine sehr schnelle Zersetzung des Stammholzes durch Weissfäule-Pilze. Ergreift die Krankheit größere Teile des Baumes, so führt dies zum Tode infolge der Unterbrechung der Nährstoffleitung oder der Baum bricht infolge der Zersetzung des Holzes um. Während man in früheren Jahren zwar gelegentlich auch solche Schäden beobachtete, ihnen aber keine grössere Aufmerksamkeit schenkte, tritt die Krankheit seit einigen Jahren in grösserem Umfang in verschiedenen Ländern (z. B. Dänemark, Deutschland, Schweiz) auf und führt hier zu sehr erheblichen Verlusten, da das wertvolle Nutzholz der starken Bäume in kurzer Zeit zu minderwertigem Brennholz wird. Eine der europäischen Buchenrindenfäule sehr ähnliche Erscheinung wird in zunehmendem Masse auch im nordöstlichen Amerika an *Fagus grandifolia* beobachtet. Während aber in Amerika die Krankheit ausschliesslich auf den Befall der Bäume durch die Buchenwollaus (*Cryptococcus fagi*) und nachfolgende Infektion durch *Nectria coccinea* zurückgeführt wird (EHRlich 1934), ist in Europa der typische Krankheitsablauf ein etwas anderer. Auf Grund umfangreicher Beobachtungen in deutschen Forstrevieren und anatomischen sowie physiologischen Untersuchungen wird der Ablauf der Erkrankung, wie er sich in deutschen Buchenbeständen vollzieht, geschildert. Sodann werden die kausalen Zusammenhänge zwischen Insektenbefall, Pilzinfektion, Rindenfäule und Klimaeinwirkung diskutiert. Die Untersuchungen ergeben auch interessante Einblicke in die Abwehrmassnahmen des lebenden Baumes und die noch wenig erforschten Luft- und Wasserverhältnisse im stehenden Stamm.

Discussion

W. P. K. FINDLAY: I may here state that a similar disease occurs in England especially

on chalk hills, the disease having much more severe effects on trees growing on steep slopes where soil is thin, than on trees growing on a good deep soil. The importance of predisposing physiological causes must be agreed but the exact role of the fungi which have been isolated must be investigated further.

N. F. BUCHWALD: Dr. Zycha has told us that the black spots (Rindenfäule) occurred in connection with the severe winter 1939-40. Do you also find the spots in connection with the winters 1940-41 and 1941-42, which at least in Denmark were just as severe as the winter 1939-40?—In our paper (THOMSEN, BUCHWALD and HAUBERG) we do not state that Rindenfäule is due to the attack by *Cryptococcus* or *Nectria*, we only say that we often find the spots in connection with *Cryptococcus*.

H. ZYCHA: Die Winter 1940-41 und 1941-42 waren in Deutschland etwas weniger streng als 1939-40. — Es gibt Buchen mit *Cryptococcus* ohne Rindenfäule und Buchen mit Rindenfäule ohne *Cryptococcus*.

Literature

ZYCHA, H. 1951. Das Rindensterben der Buche. — Phytopathologische Zeitschrift, 17, 4, 444-461.

F. L. HOWARD and J. G. HORSFALL
(Kingston, R. I.)

Concepts and Progress in Plant Chemotherapy

The principle of chemotherapy is to supply the plant with chemicals that assist in overcoming disease. Thus, a chemotherapeutant is a substance which directly or indirectly acts internally to control plant disease. In the case of wilt diseases prevention of parasitism and of pathogenesis is the mode of chemotherapy. Parasitism may be eliminated by direct parasitocidal action, or by making the host distasteful. The latter may be accomplished by changing host material used as fungus metabolites or by causing modification of cell wall composition. In so far as pathogenesis is caused by toxins it may be avoided by preventing formation of

toxins by the pathogen or by the irritated host, by checking translocation of toxins into the host tissues and by antidoting toxins excreted by the pathogen or by the irritated host.

Two distinct conditions may develop in plants from the action of toxins; protoplast necrosis, and wilt. A metabolic product that directly causes injury or death to plant cells may be termed a "necrogen," and one that causes wilt a "hadrogen." The nature of these toxic complexes may be: a pathogen metabolite, a metabolite of a diseased host, or a product of pathogen or host degeneration. The action of these toxins may proceed in different ways: by bringing about permeability changes in the host cell, by interfering with processes through which one or more cellular metabolites normally go, by altering the physical or chemical state of the host protoplasm, or, by plugging the vascular system with callus, tyloses, polysaccharides, resins, gums, and pathogen cells. The details are difficult to demonstrate *in vivo*. The primary irritant factor generally initiates a chain reaction in the cellular physiology whose components overlap.

The loci where injury occurs and where the chemotherapeutant may act require consideration in selecting the type of agent and the method of application. The living cells of the vein endings are vital to the normal functioning of the transpiration stream in trees and hence are often critical in systemic wilt diseases. Injury to the cambium or ray-parenchyma cells stops or checks differentiation of secondary tissues with resultant morphological and physiological dislocation. External differentially absorptive surfaces and root cortical parenchyma are vulnerable to the action of toxins. The sap-conducting tissues may become mechanically blocked, as is too often assumed, when wilting occurs. For therapy, antidotal chemicals can be supplied to the plant by direct stem injection, foliage application and intake, soil surface coverage or drench, incorporation in the soil by cultivation, and hydraulic soil impregnation in suspension or solution.

Three types of chemotherapeutants for wilts

can be postulated; antitoxin, antimetabolite and antipenetrant. An antitoxin inactivates toxins, an antimetabolite interferes with a process through which a metabolite normally goes, and an antipenetrant by impregnation, accretion or filming of the cell wall prevents translocation of the toxin or ingress of the pathogen to injure the host protoplast. Research is extending the principle of chemotherapy to tumefaction, virus and nematode diseases.

Discussion

E. VAN SLOGTEREN: We cure a physiological disease of the tulips by application of a 1 per

cent solution of calcium nitrate.—Can you tell us something of the curing of virus diseases as described by E. N. STODDARD? We have tried his chemicals as far as we could get them, but had no satisfactory results.

F. L. HOWARD: I have seen the experiments of Mr. STODDARD whereby he inactivated the peach X-virus with 8-hydroxyquinoline benzoate and was impressed with their validity. No general claims for cure of virus diseases have been made. Believing that the action of chemotherapeutants is usually quite specific, it does not necessarily follow that tulip viruses would be inactivated.

SESSION 3

Jointly with Section GEN: July 17th, 2—5 p.m., Attendance: 60 members

Chairman: C. SYRACH-LARSEN, Recorder: E. BJÖRKMAN

SUBJECT:

Forest Genetics Problems

C. SYRACH-LARSEN (Hörsholm, Denmark)

Tree Displays

Geneticists and botanists can regard with satisfaction a long series of wonderful results, which have been achieved in plant breeding for agriculture and horticulture by their fundamental work during recent generations. One might almost go so far as to hope that success has become so common that more workers may be tempted by the new and more "difficult" problems of tree breeding for forestry.

The task is a new and interesting one, but it is by no means certain that its difficulties are very great, and *we should not lament the slow succession of generations which such work involves, but rather rejoice at the long life of the individuals we handle.* If we discover valuable individuals we shall be able to make use of them for long periods. By means of vegetative propagation it becomes possible to employ them in seed-source-gardens (tree-orchards) and they

are ideal for long-term studies of individual peculiarities.

A tree-display is a collection of planted groups of trees, each group of which represents a clone. Tree-displays provide a "short-cut" for the forest tree breeder in his effort to arrive at an estimate of the value or utility of the genotype. They can be maintained for many years and can be so established as to make them ideal places for genetical, physiological, pathological, and other important studies. In making the necessary comparison of individual peculiarities some may hold that the only sound basis for comparison is through cuttings, layers, and other true clones. In such an important and difficult genus as *Pinus*, the possibility exists, however, of using grafts for the same purpose, the stocks employed consisting of clones of *Pinus radiata* propagated from cuttings. In addition, it would appear that successful grafting on uniform stocks even when these are grown from seed can be of great assistance.

It is true that in that event the roots are hereditarily different, but it may be no less difficult to avoid even greater physiological differences between stocks propagated from cuttings when that propagation is not easily accomplished. In tree-displays the individuals can be compared in the same area and any individual can be subjected to varied environmental conditions, as may be desired. Tree-displays may be used too in investigations concerned with the correct sub-division of species into climatic races (provenances). (Cf. CLAUSEN, KECK and HIESBY: Regional differentiation in plant species, 1941.) In such areas it should also be possible to carry out detailed plant-physiological research-work with a view to finding those individuals which live and work most economically, e.g. those which stand most shade. Then again, plant pathologists will not only be able to isolate those individuals which are most resistant to disease, but will have an opportunity of observing the behaviour of the disease under various environmental conditions. The very great value of being able to use the same individuals for investigations of this kind must be obvious.

Discussion

Å. GUSTAFSSON: It has often been said that graftings of spruce give rise to Dauer modifications only, having an abnormal type of growth. What is your experience in this matter?

C. SYRACH-LARSEN: In order to obtain grafts of spruce with a normal type of growth, we use small grafting material. Should we want early and rich flowering, we use larger branches and older stems, on which the graft is able to grow like a branch of the original tree.

P. C. NIELSEN (Hørsholm, Denmark)

Experiments with Controlled Pollinations within the Genus Fagus

During the years 1948-50 some work on the beech was carried out at the Hørsholm Arbo-

retum under the guidance of Dr. C. SYRACH LARSEN, as part of the forest tree breeding work of the Royal Danish Veterinary and Agricultural College.

Observations of the flushing, flowering and development of the fruit of *Fagus sylvatica* L. are described and it is shown that while this species is normally metandric the influence of the prevailing weather is great.

Mention is made of a small experiment with isolated emasculated twigs. The flowers did not develop kernels, but the involucre and the shell of the nuts were externally identical with those in the pollinated bags. Also the June-drop was similar. *Fagus sylvatica* is parthenocarpous.

A short description of the technique of isolation and pollination follows. In 1948 there were some initial difficulties. Apart from three cases noted during the isolation in which the flowers were very advanced, the rest of the self-pollinations (three trees with 450 nuts) yielded 2 per cent with kernel.

More stress was laid on a proper isolation in 1949. Self-pollination of 1432 female flowers on five trees resulted in two full and 487 barren nuts, while open pollination gave about 25-45 per cent fully developed nuts. Controlled pollinations of female flowers at various stages of development indicate that isolated flowers are receptive at least 7-10 days after the stigmas commence recurving.

As the self-pollinations were carried out on bagged twigs out of doors, the two good nuts in 1949 may be due to "false" pollination, that is—*Fagus sylvatica* is probably self sterile, at least self-pollination only takes place to a very limited degree.

Some crossings of *Fagus sylvatica* × *Fagus orientalis* (Lipsky) were carried out in 1948. The harvest consisted of 1026 nuts with and 361 without kernels. Seven *Fagus sylvatica* trees were used as mothers and four *F. orientalis* as pollinators. The facility with which this crossing takes place is shown by the following example—the percentage of full nuts from one tree being:

Self-pollinated	4
Open pollinated	54
× <i>F. orientalis</i>	66

Furthermore the cross *F. sylvatica* × *F. grandifolia* Ehrh. was attempted but it is not yet possible to state whether the crossing succeeded, the air and branches being full of foreign pollen when the isolation was carried out.

Discussion

D. V. BAXTER: The American forester has been greatly interested in the high quality and good form of beech grown in Denmark. The form is better than the *Fagus* we have in the United States. Is the objective of this study to obtain an even better form for Danish beech or is it the hope to produce a plant that is resistant to frost or fungi?

P. C. NIELSEN: We intend to obtain beech with faster growth and better form.

H. JOHNSON (Källstorp, Sweden)

Species Hybrids in Forest Tree Breeding

Species hybridization involves greater possibilities in forest trees than in most other cultivated plants on account of the following main conditions:

1. In most forest tree genera a fairly large number of closely related species exists, which it is possible to hybridize.
2. The yield comes from the vegetative system.
3. It is often easily possible to raise very large hybrid populations thanks to the high individual seed production, which can be increased indefinitely by means of vegetative propagation.
4. The forest trees are as a rule allogames and as such often self-sterile.
5. Some forest trees are dioicous, most of them monoicous and easy to emasculate.

By species hybridization two purposes can be realized: (1) increase in rate of growth and

(2) valuable combinations of characters from the parent species. F_1 -hybrids have been produced especially within the following forest tree genera: *Picea*, *Pinus*, *Larix*, *Abies*, *Populus*, *Betula*, *Alnus*, and *Quercus*.

A considerable increase in rate of growth has in several instances been attained. Thus six years old F_1 -populations of *Populus tremuloides* × *tremula* have reached a height of more than 7 meters as compared with 3–3.5 meters for pure *P. tremula* progenies. Certainly the rapid growth of this hybrid does not depend entirely upon heterosis but also on the fact that the hybrid is resistant to leave-destroying fungi and perhaps that the southern origin of the *tremuloides*-mother in comparison with the latitude of the place of cultivation (56° Lat.) has some influence in growth promoting direction.

Hybrids between *Betula papyrifera* and, respectively, *B. verrucosa* and *B. pubescens* grow faster than the European species but the North-American parent grows as fast as the hybrids. However, the hybrids are of greater value than *B. papyrifera* because of better quality.

The condition for utilizing a species hybrid (F_1) for reforestation purposes is either that the fertility of the species cross is high enough to permit production of the hybrid on a large scale or that the hybrid can be propagated vegetatively in an easy and cheap way. F_1 -populations of up to 40 000 individuals have been raised of the hybrid *Populus tremuloides* × *tremula*. Especially in areas where natural regeneration is practised the fertility of the F_1 -hybrid and the variation in the F_2 and other hybrid derivatives are of great interest. One of the following conditions may prevail:

1. The F_1 is completely sterile and no self-regeneration is to be expected.
2. The F_1 is more or less fertile but gives a very weak progeny, which is unable to compete with other self-regeneration. The self-regeneration from the F_1 plantation is thus without any importance.
3. The F_1 gives a vital progeny, which in

its entirety is inferior to the F_1 . This regeneration is undesirable and ought to be prevented.

4. The F_1 gives a vital progeny of which a sufficiently large fraction for giving rise to a good stand is as good as the F_1 . This regeneration is, of course, desirable and the F_2 is usable both for natural and artificial regeneration.

Discussion

D. V. BAXTER: The production of fungus-resistant trees is most important. When resistance has been obtained in some trees, however, it is sometimes a problem for the forester to know how to establish the tree over thousands of acres of land where susceptible "forms" grow in large quantities. Aspen is an example in America.

H. JOHNSON: In Sweden we have a forest area of about 20 million hectares, approximately some 14 million of which are self-regenerating. It might be difficult to introduce improved strains in the self-regenerating forests. But, of course, no difficulties at all are connected with the use of improved strains on our artificially re-forested area of some 6 million hectares. In Denmark the situation is still more favourable as all forests are artificially re-forested there.

C. L. KIELLANDER (Källstorp, Sweden)

Induced and Natural Polyploidy in Picea Abies (L.) Karst.

At the Forest Tree Breeding Institute at Ekebo colchicine treatment of germinating seeds of *Picea Abies* (L.) Karst was performed in 1941 and 1942. The treatment resulted in a varying frequency of slow-growing seedlings with short, thick needles. The highest frequency was obtained after treatment during 2-4 days with concentrations of 1.25-1.50%. Chromosome numbers of root-tips and length of stomata have been determined. The stomata measured about 32 units of the ocular micrometer in shoots with thick needles, 25

being the normal rate. The tetraploid chromosome number, $2n=48$, was often stated. Mixoploidy was common.

In 1945 an aberrant with the same deviating habit as in C-treated seedlings was discovered among 570 000 2-year-old seedlings. The suspicion suggested itself that this could be a spontaneous polyploid. Ever since, such aberrants have been searched for during the sorting always undertaken with 2-year-old seedlings. The following spring 93 aberrants were picked out from among 1 200 000 seedlings. Of these 49 were diploid with $2n=24$, 1 was triploid with $2n=36$, 22 were tetraploid with $2n=48$, 3 were mixoploid.

This material derives its origin from a batch of seed collected from about 500 trees. Later on new aberrants have been discovered among the progeny from many different mother trees. The frequency was also in this case very low.

These natural polyploids do not differ morphologically from C_0 plants of the same age, and have the same poor growth. In forest nurseries they will certainly be discarded at the latest when 4 years old. In plantations and dense natural reproductions they are doomed. In thin natural reproductions they will probably be able to live on for some time but only in gaps in the stands they can develop further. In Helsingfors there is a spruce 1 metre high to be seen where the needles have the typically tetraploid appearance. The spruce was discovered in 1941 and had been growing in "a little opening in a fairly old spruce stand." It is labelled *Picea excelsa* f. *brevifolia*.

From the present investigation the conclusion is drawn, that deviations from the normal chromosome number often results in a different morphological type. In mercantile nurseries slow-growing spruces have since long been sold as dwarf spruces, which often resemble the thick-neededled tetraploids. Possibly some of these forms of spruce known by different names are just polyploids and aneuploids.

The purpose has been to produce rapid-growing polyploids. The natural polyploids,

however, make it likely that triploid and tetraploid spruce races are more slow-growing than diploids. In *Picea Abies* $2n=24$ certainly represents the chromosomal optimum. This explains why tetraploidy in spruce has hitherto escaped detection.

S. S. PAULEY (Petersham, Mass.)

Work of the Cabot Foundation

Forest-tree genetic research was first formally recognized at Harvard University with the establishment of the Maria Moors Cabot Foundation for Botanical Research in 1937 by Dr. GODFREY L. CABOT of Boston. Since that time a number of basic studies have been undertaken, employing the valuable botanical collections or facilities afforded by other units of the University, especially the Arnold Arboretum, Bussey Institution and the Harvard Forest.

The principal lines of investigation upon which the attention of the Cabot Foundation is focused include: (1) studies of natural variability within various tree genera and species; (2) inter- and intraspecific hybridization studies, tests of such hybrid progenies, and the testing of various hybridizing techniques and methods for the induction of early flowering; (3) asexual propagation; (4) studies designed to determine the degree of correlation existing between the expression of certain juvenile and adult characters in trees; and (5) disease and insect resistance investigations.

Studies of natural variability have to the present been undertaken by the Cabot Foundation in three forest genera: *Populus*, *Quercus*, and *Pinus*. The greater accumulation of material thus far assembled is confined to the native aspens and poplars of the genus *Populus*.

Clonal line ecotypes of most native poplar species in our collections now number more than 2000. On the basis of preliminary observations it is apparent that there are marked variations between clones of different geographic origin which must be attributed to genetic differences. Many conspicuous variations

are related to the timing of certain physiological functions, especially time of leaf emergence and time of growth termination in the autumn. Morphological variability is also a marked feature within some native poplar species, especially in the section *Aegeiros*. Our studies will likely aid in the clarification of the confused taxonomy within this group.

Hybridization studies have been confined chiefly to the genus *Pinus* and *Populus*. Most inter- and intraspecific F_1 -hybrids within these genera have demonstrated heterosis; but some rapid growers are otherwise undesirable because of disease susceptibility or poor form.

Vegetative propagation of difficult species has been given considerable attention by workers in the Cabot Foundation. A book summarizing the work with auxins done by this Foundation and numerous other investigators in this country and abroad was recently published. Studies of the correlation existing between juvenile and adult characters in trees have been under way for several years. Most of this work is confined to the poplars and is concerned chiefly with growth rate and stem form.

Disease resistance studies have been undertaken cooperatively with the United States Department of Agriculture, Bureau of Plant Industry. Interest is directed primarily to the isolation of wild immune or resistant individuals (possessed of other desirable characters as well) which may be used for breeding stock.

H. VAN VLOTEN (Wageningen)

Tree Diseases in Relation to Provenance

The problem of provenance and disease cannot be considered fully understood in spite of many literature references. It even constitutes an example which proves the need for close international cooperation. The International Botanical Congress may contribute to such a cooperation.

Referring to literature (BOYCE 1941, FISCHER 1950, DAY 1923, 1948, 1949, DAY and PEACE 1934, WATERMAN 1939, BAXTER 1937)

one may state that in order to understand the relation between tree diseases and provenance, it is most important to consider the problem of *tree diseases in relation to provenance of forest pathologists*. Pathologists are looking at the relation tree diseases: provenance from their own, more or less national, angle.

One reason for this originates from the different treatment of the experiments, the different way to measure or to record the results. As to the needle shedding of Scotch pine by *Lophodermium Pinastri* CHÉV. most research workers, like MÜNCH (1949), have been waiting for the accidental natural infection by the fungus. KALELA (1937), on the other hand, used a kind of artificial inoculation to compare three provenances. Do we need elaborate plant tests as applied in Dutch experiments with *Pinus Strobus* of different origin and *Cronartium ribicola* (VAN VLOTEN 1939, 1941)? Or is the knowledge of the resistance under conditions of forest practice sufficient? Both are necessary. This is certainly true, if strains of parasites are involved. The poplar rust caused by *Melampsora larici-populina* KLEB. (VAN VLOTEN 1944) is an example of this.

One other difficulty is raised by the valuation of the influence of site factors, soil, climate, and silvicultural treatment, on the occurrence and effect of diseases. In several publications DAY stated that *Phomopsis Pseudotsugae* Wilson on Japanese larch is a secondary organism, following only the effect of frost damage. An extensive experiment carefully carried out by the Forest Research Station T. N. O., Wageningen, however, shows clearly that—at least in the Netherlands under conditions of these experiments—*Phomopsis* is a true parasite on Japanese larch and not "colonizing parts of the bark killed by frost". But it is by wounds only that the fungus is able to infect. These wounds have proved to be dangerous when made during the resting season; during the growing season from May till August they are harmless; during that time of the year the trees recover too quickly to give the parasite a chance.

The way out of such contradictory items and difficulties will be a closer contact and international cooperation between forest pathologists. For the same purpose the International Union of Forest Research Organizations has formed eleven sections covering different branches of forest research. One of these, number 24, is treating "forest protection". Participation by research organizations and research workers concerned is welcome. This will give an opportunity for valuable discussions, joined efforts, team-work of different countries and, if necessary, prevention of unnecessary duplicates.

Discussion

D. V. BAXTER: The question of planting exotics in the United States has centered largely about the culture of trees from foreign lands. It is of importance for us to understand if trees do not recognize political divisions. The matter of site is of greatest significance. We, in Michigan, for example, have certain barren sites that resemble those in Arizona more than they do areas that are more typically eastern. *Pinus ponderosa* from Arizona (a distant state) grows more satisfactorily on those sites mentioned in Michigan than does *Pinus strobus*, a Michigan native.

C. SYRACH-LARSEN: I may here give a few examples, illustrating the same thing. *Pinus radiata* is a tree which is not very common in California. In New Zealand it has some 50–60 times as vast a distribution under artificial culture. 25 year-old planted trees may have a height of 40–41 meters.—*Quercus palustris* from Eastern U.S.A. is the most suitable tree for growing in the streets of the dry city of Canberra in Australia.

O. LANGLET (Stockholm)

Die praktische Verwertung der Provenienzversuche in Schweden

Die forstliche Versuchsanstalt hat Versuchsflächen mit Kiefern und Fichten verschiedener

Provenienz, von denen die ältesten jetzt mehr als 40 Jahre alt sind. Als Folgerung der Resultate, die diese Flächen gegeben haben, verglichen mit den Resultaten anderer Provenienzversuche, sind die zulässigen Grenzen der Versetzung von Samen und Pflanzen von Kiefer und Fichte in verschiedenen Richtungen von der Heimat der betreffenden Provenienz provisorisch festgelegt worden.

Discussion

H. VAN VLOTEN: Was denkt Dr. LANGLET von der *Pinus silvestris* var. *lapponica* im Zusammenhang mit den gleitenden Übergängen? Ist sie nur noch ein theoretischer Begriff?

O. LANGLET: Betreffe *Pinus silvestris* var. *lapponica* gibt es klimatökologisch keinen scharfen Übergang von den südschwedischen Kiefernprovenienzen.

A. F. VON DER SCHULENBURG (Hamburg)

Provenienzfagen bei Zellstoffhölzern

Picea Abies, die Fichte, ist Europas Papierholzlieferant Nr. 1, ihre Wuchsförderung daher sehr aktuell. Interessant wurde infolgedessen auch die Erfahrung, dass mitteleuropäische Berglandfichten beim Verbringen nach Nordeuropa die dort einheimischen Fichten an schnellerem Wuchs merklich übertrafen. Grund: Die Fichten aus dem Kurztaggebiet können im Langtaggebiet täglich die sommerliche Vegetationszeit hindurch einige Stunden länger assimilieren. Ein Nachteil zeigte sich indessen, nämlich dass Berglandfichten aus Mitteleuropa (Harz, Thüringen, Schwarzwald usw.) in Flachlandgebieten des Nordens zu früh im Jahre aus dem Winterschlaf geweckt werden. Sie treiben daher zu zeitig ihre jungen Triebe aus und fallen in Frostlagen jahrzehntelang den Spätfrösten zum Opfer. Folge: Erhebliche Zuwachsverluste, oft Krüppelwuchs. Ein kleines, uraltes Tieflandfichten-Reservat, Pforten, wurde vom Referenten 1926 entdeckt und danach in jedem guten Samenjahre zur Aberntung veranlasst, denn diese Klimarasse

erwies sich als vollkommen spätfrosthart. Das erwähnte Reservat und die umfangreichen Absaatkulturen des Referenten gingen im letzten Kriege und den folgenden Jahren verloren, aber in Dänemark sind glücklicherweise noch Vergleichsabsaaten davon vorhanden aus Saatgut, welches der Referent 1936 dorthin zu Händen des staatlichen Versuchswesens stiftete. Von dort aus sind nun Vermehrungen durch Veredlungsreiser in Schweden und Westdeutschland in die Wege geleitet.

Wo auf frischen Lehm- und Mergelböden anstatt der bodenständigen Laubhölzer zum Beschleunigen der Holzmassenerzeugung Fichte angebaut wurde, zeigte sich oft und frühzeitig Holzentwertung durch Rotfäule. Noch schnellwüchsiger und gleichzeitig immun gegen Rotfäule erwies sich aber auf solchem Standort die amerikanische Lodgepole pine. Nach der letzten U.S. Forest Service-Nomenklatur heisst sie botanisch: *Pinus contorta latifolia* (syn. *P. Murrayana* BALFOUR). Diese Lodgepole pine (Murraykiefer) wurde in Grossversuchen in Mustila, Südfinnland, angebaut. Sie ergab auf annehmlichen Böden in 33 Jahren auf gleichalten, benachbarten Flächen folgende Erträge je Hektar:

Finnische Fichte 160 m³

Finnische Kiefer 210 m³

Lodgepole pine 320 m³.

(Hier stammte die Lodgepole pine aus nordwestamerikanischer Provenienz, Canada.)

Die wichtigsten Voraussetzungen für diese überragenden Wuchsleistungen der Lodgepole pine sind:

a) Strengste Beobachtung der Saatgutprovenienz aus Nordwestamerika, angepasst an das entsprechende europäische Lokalklima.

b) Guter, frischer bis feuchter Laubholzboden, Grastyp. Ungeeignet: saure Podsolböden, trockne Sande oder versumpfter Boden.

c) Lodgepole pine soll nicht in eng stehenden Monokulturen angebaut werden, sondern zur Hälfte bis zu zwei Dritteln mit langsamer wachsenden anderen Holzarten gemischt in weitem Abstände. Dazu verwendbar: *Picea*

sitchensis, *Picea Abies* usw., besser aber Laubholz, wie *Alnus incana* oder *A. glutinosa*.

Discussion

C. L. KIELLANDER: In addition to the paper just read, I should like to point out the importance of late sprouting spruces in Sweden. From the Institute of Forest Tree Breeding some progeny tests in South East Sweden demonstrate this fact, as most progenies from native spruces have not more than about 50 cm total height after 10 years and repeated spring frosts. On the other hand, progenies from pure German spruces (planted in South Sweden) which have never been damaged by frost, have a total height of up to 2 meters. In South Sweden up to the latitude of Stockholm the German spruce probably grows better than the native one and it will certainly in the future become very wide-spread and simultaneously tested. German spruce is certainly not hardy in northern Sweden, and probably not even at higher altitudes in southern Sweden.

H. ROBAK: May I here only mention the excellent growth of the spruce of the Pforsten provenance in the International spruce test plot in Western Norway.

C. HEIMBURGER (Maple, Ont.)

The Breeding of White Pine (*Pinus Strobus* L.) in Canada

White pine is one of the most valuable forest trees in North America. In recent years attacks of blister rust (*Cronartium ribicola* J. C. FISCHER) and weevil (*Pissodes Strobi* PECK) have greatly discouraged its use in intensive forestry. The selection and breeding of biotypes showing a high degree of resistance to these agencies and superior timber producing capacity is a most important forest tree breeding project. Such a project was initiated

by the Dominion Forest Service in cooperation with the National Research Council of Canada and the Dominion Department of Agriculture in 1937 and by the Ontario Department of Lands and Forests in 1946. After the war contacts have been reestablished with forest tree breeders in Scandinavia and grafting introduced as a useful tool. White pine lends itself exceptionally well to the standard grafting technique on potted stock under glass in late winter, early spring and fall, and to outside grafting. It has been possible to graft white pine on Scotch pine (*Pinus silvestris* L.) and jack pine (*Pinus Banksiana* LAMB.). Partial girdling has been found promising for the stimulation of flowering in stands of polewood size. White pine crossings with related species are being studied. The glabrous young shoots of *P. Peuce* GRISEB. are dominant in hybrids with white pine, while those of *P. excelsa* WALL. are recessive. Evidence is at hand for a high degree of resistance to blister rust within several populations of white pine. No evidence has as yet been found for resistance to weevil. Native populations are sampled by means of seed collections and scions from elite trees that show superior growth rate and form, and are free from blister rust and weevil attacks under conditions of severe infection. The material is being subjected to inoculations with blister rust during several successive years, using grafts from susceptible trees as controls. Outside grafting is promising in testing for resistance to weevil. Young plantations have been established for this purpose in close proximity to severely weeviled older white pine. Material of species crossable with white pine, and of some hybrids, is being assembled for testing and evaluation. Several of these are known to possess resistance to blister rust, and their evaluation in terms of resistance to weevil attacks may also yield important information.

The paper was read by A. E. PORSILD.

SESSION 4

July 18th, 9 a. m. — 1 p. m., Attendance: 35 members

Chairman: E. EIDE, Recorder: E. BJÖRKMAN

SUBJECT:

Forest Ecology

The Session decided to send telegrams to the following absent members of the Section:

To Professor Dr. JOHANNA WESTERDIJK, Baarn, Netherlands (motion made by Dr. L. HUTCHINS and Dr. K. T. CARTWRIGHT);

to Professor Dr. JOHN BOYCE, New Haven, Connecticut, U.S.A (motion made by Dr. H. VAN VLOTEN and Dr. H. ROBAK);

to Professor Dr. HANS BURGER, Zürich, Switzerland (motion made by Dr. E. BJÖRKMAN and Dr. H. VAN VLOTEN).

H. VAN VLOTEN (Wageningen)

The undersigned committee was appointed by the Chairman of the Section of Forest Botany to draft a resolution on international cooperation in the fields of forest tree breeding and forest protection.

In presenting a draft of the resolution for consideration by the Section, the committee desires to explain the possibilities for close cooperation offered by the International Union of Forest Research Organizations. The Union was founded in about the year 1891, and continued its useful work until the end of World War II. Lately there has been an important reorganization. An agreement between the Union and the FAO (United Nations Organization for Food and Agriculture) has come into force after having been prepared on the occasion of the 1948 Zürich Congress. This cooperation is developing in a satisfactory manner.

The Secretariat under the sponsorship of the Forestry Office of FAO, at Geneva, has begun to function. Thanks are due to Mr

MARCEL LELOUP, Director of the Division of Forestry and Forest Products in the Washington office of FAO, and to Mr D. CAMERON, Chief of the European Forestry Bureau, of Geneva, for their comprehending participation in organizing this cooperation.

We would like to add a few words about the scientific activities of the Union. In order to stimulate the exchange of technical opinion, the field of forest research was divided into eleven research sections, among which we especially call attention to Section 22, Study of Forest Plants, and Section 24, Forest Protection.

Committee:

N. F. BUCHWALD

W. P. K. FINDLAY

L. M. HUTCHINS

H. VAN VLOTEN, *Chairman*.

Resolution

The Section of Forest Botany of the VII International Botanical Congress assembled at Stockholm on the 18th of July, 1950, welcomes the establishment of active international committees to cooperate in the field of tree breeding and forest protection as provided by the International Union of Forest Research Organizations (see Annual Report of the Union for the Year 1949). The Section would welcome participation by research organizations and research workers concerned, through joining Section 22 of the Union, which deals with the study of forest plants and forest tree breeding under the leadership of Dr. C. SYRACH-LARSEN of Hørsholm, Denmark, or through joining Section 24, which deals with forest protec-

tion against damage by fungi, insects, and other natural agencies, under the leadership of Dr. H. VAN VLOTEN, Wageningen, Netherlands.

The advantages to be obtained from close cooperation of this kind among research agencies and specialists are demonstrated by many of the papers presented before the Section of Forest Botany.

V. J. CHAPMAN and R. V. MIRAMS

(Auckland)

Natural Regeneration in the Kauri

The problem of natural regeneration has been considered from two aspects: (a) occurrence, (b) factors affecting regeneration.

(a) Occurrence.

The application of quantitative methods has shown that regeneration is best under tea tree scrub and poorest under mature Kauri stands. It would thus appear that Kauri may not be able to replace itself *in situ* and is perhaps only a transient type.

(b) Factors.

An analysis of cone production and seed content shows that there is adequate seed for natural regeneration. Of the seed set 1/3-1/2 is sound but the viability of this seed is low and it drops rapidly on storage. This reduction is not due to drying out because seed stored under conditions of low humidity retains its vitality. The high humidities of the natural habitat inhibit retention of vitality. Germination is affected by light intensity and method of insertion of the seed in the soil. There do not appear to be any germination inhibitors in the natural habitat. There is a very considerable mortality of sound seed on the ground caused by a large insect, the weta.

Discussion

D. V. BAXTER: These studies emphasize the importance of certain biologic factors of site in regeneration.—I should like to inquire about the extent of these forests in New Zealand.

V. J. CHAPMAN: Four large stands now re-

main in different parts of New Zealand. The present work was carried out in the Auckland City Water Reserve.

M. S. PARRY: As the Kauri forest is believed not to be the true climax of the area, are there any indications as to the cause, either of its comparatively recent origin, or of its failure to develop into the true climax?

V. J. CHAPMAN: The Kauri is very long living and man has only recently occupied New Zealand and the evidence is purely circumstantial.

R. DAUBENMIRE: Have light requirements been studied in an effort to explain the failure of Kauri germination after the forest develops?

V. J. CHAPMAN: It is said that Kauri needs shade when young and light later. Experiments are now being carried out to acquire quantitative data.

L. HUTCHINS: Dr. Chapman stated that the Kauri trees may live to 1000 years of age. I should like to know whether they are susceptible to rots of root or stem or other destructive diseases.

V. J. CHAPMAN: Kauri is relatively resistant to disease now that gum-tapping is prohibited. It succumbs under swampy conditions.

H. VAN VLOTEN: Is there any trial to get the area of Kauri extended by artificially culturing the tree outside its natural range?

V. J. CHAPMAN: No attempts have so far been made to establish Kauri plantations.

R. DAUBENMIRE: If Kauri seeds normally germinate at once upon dissemination, how can their failure to retain viability for a long time be used in explaining the failure of germination?

V. J. CHAPMAN: Some seed is probably not mature at seedfall and would lose its viability before it germinated.

W. VON WETTSTEIN (Wien)

Über die Blütenbiologie unserer Waldbäume

Die Tatsache, dass die Veredlung nutzholzliefernder Bäume der Erde allgemein als not-

wendig erachtet wird, bringt es mit sich, dass auch die Biologie ihrer Blüten eingehend beobachtet wird. Jeder Kreuzungsarbeit muss auch eine genaue Kenntnis der Befruchtungsdauer vorausgehen. Schon 1938–1940 haben DENGLE und WETTSTEIN Beobachtungen über den Beginn und das Abblühen der weiblichen und männlichen Infloreszenzen von *Pinus silvestris* durchgeführt. Die Pollenreife kann an abgeschnittenen Zweigen nach Belieben reguliert werden. Die Empfängnisdauer am natürlich gewachsenen Baum jedoch ist wesentlich von der Umwelt und genetischen Faktoren abhängig. Die Prüfung erfolgt nun in der Weise, dass vor dem Aufblühen etwa 100 Infloreszenzen isoliert werden und dann täglich eine bestimmte Anzahl auf 24 Stunden der freien Befruchtung ausgesetzt werden. Es ergab sich nun eine Empfängnisbereitschaft für *Pinus silvestris* und *Pinus nigra* von 7–9 Tagen, für *P. montana* ssp. *Pumilio* von 5–6 Tagen, für *Larix europaea* von 9–10 Tagen, wobei Regen- und Schneeböen eine Unterbrechung von 4 Tagen ergaben. Die Beobachtungen wurden an 3 Herkunft gemacht. Bei *Tilia platyphyllos*, wo es sich um die Aufblühfolge in den Dichtungen handelte, wurde teils die kastrierte Mittelblüte 24 Stunden der Insektenbestäubung überlassen, teils die Mittelblüte entfernt und die kastrierten Seitenblüten der natürlichen Bestäubung je 24 Stunden überlassen. Die Periode der Blütendauer ist deutlich zweigipfelig. Die Mittelblüte ist 4 Tage (10.–13. Juni) empfangsfähig und die Seitenblüten nach einem Zwischenraum von 3 Tagen ebenso 4 Tage empfangsbereit. Die Meinung der Praxis, dass eine Rassentrennung bei Koniferen durch den Ferntransport von Pollen nicht möglich wäre, hätte bei einer Empfängnisbereitschaft von 8 Tagen wohl ihre Berechtigung. Nun hat ROSENKRANZ 1946 auf Grund phänologischer Beobachtungen feststellen können, dass der Vollfrühling in den Niederungen des Wiener Beckens nur 50–60 km in einer Woche vordringt und in den Gebirgstälern sogar nur 10 km in 7 Tagen. Da es klar ist, dass bestandes-eigener Pollen durch seine Masse massgeblicher

wirkt als der fein verteilte von fern hertransportierte Pollen, wird eine Rassenmischung nur bei einer künstlichen Bestandesgründung mit Einbringung fremder Provenienzen möglich sein. Die beschränkte Blütezeit ist für die Ausbildung von Ökotypen von ausschlaggebender Bedeutung. Die immer wieder beobachtete Konstanz einzelner Rassen ist sicherlich auf die Dauer der Empfangsbereitschaft der weiblichen Blüte zurückzuführen.

Discussion

H. VAN VLOTEN: Ich bitte um eine nähere Erklärung über die individuelle Variation innerhalb einer Rasse. Habe ich es richtig verstanden, dass die individuellen Variationen nicht grösser sind als die Unterschiede zwischen allen untersuchten Rassen?

W. VON WETTSTEIN: Die Empfängnisdauer innerhalb einer Rasse von Kiefern kann sich individuell um 4 Tage verlängern bzw. verschieben. Eine grössere Differenz wurde bisher bei den Herkunftsversuchen in Eberswalde und in Österreich nicht gefunden.

R. DAVID (Bordeaux)

L'utilisation des »Hormones de Synthèse« pour la protection de la forêt landaise contre l'incendie

Les végétaux du sous-bois (Brande, Bruyères, Ajoncs, Molinie) sont les agents de propagation de l'incendie. Quoique certains auteurs pensent que leur présence peut exercer une influence favorable sur la vie du Pin maritime (réalisation possible d'un équilibre biologique entre le Pin et les espèces du sous-bois), il n'en demeure pas moins que la présence de ces végétaux constitue une menace de destruction de la Forêt. Dans ces conditions, le débroussaillage devient une nécessité.

D'après nos travaux, il semble bien que le danger d'incendie peut être considérablement amoindri si un débroussaillage mécanique

est suivi de pulvérisations périodiques de produits du type hormone de synthèse.

Ainsi, des pulvérisations de solutions aqueuses de 2-4 dichlorophenoxyacetate de sodium possèdent une action insuffisante sur les espèces du sous-bois. Par contre, si l'on ajoute à ces solutions une certaine quantité d'une huile minérale émulsionnable, on provoque la destruction des parties aériennes des Brandes, Bruyères et Ajoncs (2,4-D 2,7 à 5,4 ‰, huile minérale: 0,75 %). L'adjonction d'un mouillant ne modifie guère les résultats. Les Graminées ne sont pas touchées par le traitement.

Au printemps suivant, quelques rejets apparaissent sur les souches des Brandes et Ajoncs, mais la vitalité de ces sujets—surtout des *Ajoncs d'Europe*—paraît sensiblement diminuée par rapport à des témoins débroussaillés mécaniquement. De nouvelles pulvérisations sont effectuées cette année sur les mêmes parcelles de manière à rechercher si on peut obtenir cette fois la destruction des parties souterraines.

D'autre part, une série d'essais effectués tous les mois a permis de constater que l'acide 2,4-D utilisé sous diverses formes commerciales est tout particulièrement actif au moment de la période de la plus grande croissance des végétaux, c'est-à-dire d'Avril à Août pour la région landaise (destruction des parties aériennes au bout de quelques jours à cette époque, tandis que 2 à 4 mois sont nécessaires pendant l'hiver).

H. BURGER (Zürich)

Der Einfluss teilweiser Entnadelung auf den Zuwachs von jungen Schwarzföhren und Fichten

Astungs- und Entnadelungsversuche an Föhren und Fichten haben folgendes ergeben:

1. Föhren sind gegen eine Verkleinerung des Assimilationsapparates weniger empfindlich als die Fichten.

2. Schneidet man alle Seitentriebe weg und belässt nur die Nadeln am Schaft, so gehen junge Fichten meistens ein, während sich ähnlich behandelte Föhren wieder erholen können.

3. Werden bei Astungen die Kronen um 50 % verkleinert, so bleibt der Höhenzuwachs bei der Föhre fast gleich und nur der Stärkezuwachs wird kleiner, während bei der Fichte auch der Höhenzuwachs schon beträchtlich sinkt.

4. Bei Föhren darf also bei Aufastungen stärker in die grüne Krone eingegriffen werden als bei Fichten.

5. Werden Föhren und Fichten während 10 Jahren so entnadeln, dass nur noch 2 benadelte Triebe verbleiben, so sinkt bei den Föhren der Höhenzuwachs nur um 2-3 %, der Massenzuwachs aber schon um 15-45 %, während bei der Fichte schon der Höhenzuwachs auf die Hälfte sinkt, der Massenzuwachs aber auf 1/4 bis 1/5 des Zuwachses vollbenadelter Pflanzen.

6. 17-jährige Föhren, die während 10 Jahren bis auf 2 Nadeljahrgänge entnadeln wurden, trugen im Mittel rund 40 % weniger Nadeln und schufen damit auch einen um etwa 40 % kleineren Zuwachs, während gleich behandelte Fichten rund 80 % weniger Nadeln trugen und damit auch einen entsprechend geringeren Zuwachs erzeugten, der aber schwerer war als bei unentnadelten Bäumen.

7. Der Versuch hat klar erwiesen, dass selbst bei den Föhren zwei Nadeljahrgänge nicht überall genügen, um den normalen Zuwachs zu schaffen und dass mehr als 2-jährige Nadeln selbst bei den Föhren, besonders aber bei den Fichten, noch tüchtig mitarbeiten.

8. Die jüngsten 1-2-jährigen Nadeln von Fichten und Föhren schaffen aber doch pro Nadelgewichtseinheit etwa 15 % mehr Trockengewichtszuwachs als die im Mittel älteren Nadeln der vollbenadelten Pflanzen.

9. Der Entnadelungsversuch zeigt, dass eine durch das Klima oder Pilze oder Insekten erfolgte Entnadelung bis auf 2 Nadeljahrgänge bei den Föhren ziemlich leicht überwunden werden kann, bei den Fichten und ähnlichen Arten, wie z. B. der Douglasie, aber erhebliche Störungen verursacht.

Der Vortrag wurde von W. VON WETTSTEIN gehalten.

Discussion

H. VAN VLOTEN: Ist vielleicht auch der Versuch etwa in umgekehrter Reihenfolge gemacht worden, so dass also die jüngsten Nadeln weggenommen und nur die älteren am Baum gelassen wurden?

W. VON WETTSTEIN: Soviel mir von den Versuchen BURGERS bekannt ist, hat er nur die älteren Jahrgänge der Nadeln entfernt und nicht den jüngsten Zuwachs, unter dem Gesichtswinkel, dass die Störung des jüngsten Zuwachses einen sicheren Abbruch ergibt.

E. AICHINGER (Arriach b. Villach)

Vegetationsentwicklungstypen als Grundlage unserer land- und forstwirtschaftlichen Arbeit

Mehrere Jahrzehnte lang habe ich die Wälder Europas in pflanzensoziologischer und forstwirtschaftlicher Hinsicht eingehend studiert. Dabei bin ich zu folgenden Erkenntnissen gelangt.

Die Anlegung von Fichtenmonokulturen ausserhalb des natürlichen Fichtenverbreitungsgebietes war ein folgenschwerer Missgriff, wie die zunehmenden Schädigungen durch Insekten, Pilze, Stürme usw. beweisen. Man muss anstatt solcher Fichtenforste und anderer herabgewirtschafteter Wälder naturnahe Wirtschaftswälder nach vegetationskundlichen Gesichtspunkten schaffen. Eine vollkommen sachgemässe und zweckentsprechende vegetationskundliche Erfassung der seit langem unter menschlichem Einflusse stehenden Wälder gelingt aber meistens weder nach der Methode der Zürich-Montpellier-Schule (BRAUN-BLANQUET), noch nach der Methode der fenno-skandinavischen Schule (DU RUIZ). Man kann sich bei unseren meist stark verwüsteten Wirtschaftswäldern nicht immer auf Charakterarten und oft auch nicht auf dominante Arten stützen. Auch können Waldbestände, die gegenwärtig die gleiche Zusammensetzung aufweisen, die Glieder ganz verschiedener Vegeta-

tionseentwicklungen sein, daher eine verschiedene wirtschaftliche Behandlung erfordern. Es muss also zunächst Klarheit darüber geschaffen werden, woraus ein jetzt bestehender Wald hervorgegangen ist und wohin er sich nach Aufhören des menschlichen Einflusses weiter entwickeln würde.

Auf diese *dynamische* Erfassung der Wälder als „Waldentwicklungstypen“ gründet sich mein „syngenetisches System“. Die von mir eingeführte Bezeichnung der Waldentwicklungstypen ist nicht ganz einfach; sie sagt aber sehr viel aus. Die Entwicklungsrichtung der Waldgesellschaften wird durch Pfeile ausgedrückt. Ein aufwärts gerichteter Pfeil (↗) bedeutet eine aufsteigende Entwicklungsreihe, ein absteigender Pfeil (↘) eine rückschreitende Entwicklung. Vom gegenwärtigen Entwicklungsstadium der Waldgesellschaft wird der Hauptname mit Grossbuchstaben geschrieben. Als Beispiel diene die Soziation eines heidelbeerreichen Fichtenwaldes. Diese kann sowohl in der Oberen Buchenstufe auftreten, wo ein ehemaliger Rotbuchen-Tannen-Fichten-Mischwald durch Streunutzung, Kahlschlag, Waldweide sekundär herabgewirtschaftet wurde (*Abietetum-Fagetum piceetosum* ↘ *PICEETUM vaccinosum Myrtilli*), als auch in der Unteren Nadelwaldstufe, wo ein solcher Fichtenwald unter einem bodensäuren Lärchenwald aufgekommen ist und sich nicht mehr weiter zum Rotbuchen-Tannen-Mischwald erziehen lässt (*Laricetum deciduae* ↗ *PICEETUM vaccinosum Myrtilli*). Auch an vielen anderen Beispielen liesse sich zeigen, dass in den Alpen unter den verschiedensten Verhältnissen des Klimas, Bodens und der forstwirtschaftlichen Waldbehandlung die gleiche Soziation entsprechend ihrer verschiedenen Entwicklung ganz verschiedene Bewirtschaftung erfordert.

Ähnlich den Waldentwicklungstypen unterscheide ich auch „Wiesenentwicklungstypen“, also allgemein „Vegetationsentwicklungstypen“. Im Sinne meines syngenetischen Systems fasse ich zum selben Vegetationsentwicklungstypus alle diejenigen physiognomisch einheitlichen Pflanzenbestände zusammen,

welche sowohl in ihren floristischen und soziologischen Merkmalen, als auch in ihrem durch die Standortverhältnisse bedingten Haushalt übereinstimmen und demselben Stadium einer Entwicklungsreihe angehören.

Demnach fasse ich die Vegetationsentwicklungstypen

1. physiognomisch-floristisch, indem ich alle Vegetationseinheiten mit gleichem Erscheinungsbild zur selben Obergruppe stelle, z. B. *PICEETUM excelsae*, und

2. ökologisch-floristisch, indem ich die Vegetationseinheiten der Obergruppen nach ihren Umweltsbedingungen zu ökologischen Gruppen vereinige, z. B. *PICEETUM excelsae basiferens*, und

3. syngenetisch-floristisch, indem ich die Vegetationseinheiten innerhalb der einzelnen Gruppen als Glieder einer Vegetationsentwicklungsreihe betrachte, z. B. *Pinetum silvestris ericosum carnea* / *PICEETUM excelsae* / *Abieteto-Fagetum*, und die Vegetationsentwicklungs-Untertypen floristisch-soziologisch, z. B. *Pinetum silvestris* / *PICEETUM excelsae caricosum albae* / *Abieteto-Fagetum*.

Insbesondere die forstliche Praxis braucht die Erfassung der Waldgesellschaften als Glieder von Entwicklungsreihen. Denn erst mit Hilfe dieses Wissens ist es dem Forstmann möglich, das eigentliche Wesen seiner Wirtschaftssubstanz zu verstehen und aus voller Erkenntnis heraus die Entwicklung zu beschleunigen, aufzuhalten und entsprechend seinem Wirtschaftsziel umzulenken, um aus dieser Möglichkeit der naturgegebenen Einfluss-

nahme nachhaltigen wirtschaftlichen Nutzen zu ziehen.

Die Aufstellung der Waldentwicklungstypen will auf keinen Fall die Assoziationen im Sinne BRAUN-BLANQUETS oder die Soziationen und Konsoziationen im Sinne der fennoskandinavischen Schule ersetzen. Nein, sie will lediglich im Interesse der Praxis die Möglichkeit bieten, dass unter demselben Namen dasselbe Wirtschaftsobjekt verstanden wird, und sie will verhindern, dass die forstliche Praxis weiterhin Erkenntnisse und Erfahrungen verallgemeinert, die an syngenetisch verschiedenartigen Objekten gewonnen worden sind.

In den einheitlicheren nordischen Ländern sind dieselben Soziationen um vieles weniger pleiogenetisch und daher die Gefahr von Fehlschlüssen geringer, als in den Alpen.

Discussion

H. VAN VLOTEN: Der forstliche Weltkongress in Helsinki im Jahre 1949 hat mit besonderem Nachdruck den Wunsch geäußert, die forstlichen Versuchsanstalten möchten sich dem Problem der Beeinflussung des Standortes durch die Holzarten (ganz besonders die exotischen) und die verschiedenen Assoziationen zuwenden.—Man darf bei den pflanzensoziologischen Beobachtungen den Baum nicht vergessen. Ich bitte hierüber den Bericht des Kongresses des Internationalen Verbandes der forstlichen Versuchsanstalten (Zürich 1948) nachzulesen, ganz besonders den Vortrag von PROFESSOR PALLMAN.

SESSION 5

Jointly with Section EXE: July 18th, 2—5 p. m., See page 250

SESSION 6

Jointly with Section MYC: July 19th, 9 a. m.—noon, See page 435

SESSION 7

July 19th, 1—5 p. m., Attendance: 40 members

Chairman: W. BAVENDAMM, Recorder: E. BJÖRKMAN

SUBJECT:

Rot Fungi and Decay Injuries

W. BAVENDAMM (Reinbek/Hamburg)
*Über die Möglichkeiten einer künstlichen
Zucht von holz- und humusbewohnenden
Speisepilzen zur Gewinnung von Eiweiss
und Heilmitteln*

Die Bestrebungen der Menschen, höhere Pilze künstlich zu züchten, sind zur Zeit noch ziemlich unvollkommen und rückständig. Abgesehen vom Kulturechampignon (*Psalliota bispora*) werden im grossen Maassstab nur noch in Japan auf Eichenknüppeln der Shiitake-Pilz (*Cortinellus Shiitake*), im fernen Osten auf Reisstroh eine Scheidlings-Art (*Volvaria volvacea*) und gelegentlich, z. B. in Frankreich, auch Trüffeln und Morcheln gezogen. Während des zweiten Weltkrieges und nachher wurde in Deutschland zur Verbesserung der schlechten Ernährungsverhältnisse u. a. die von FALCK, BUSSE und LIESE entwickelte künstliche Zucht weiterer holzbewohnender Speisepilze, wie besonders des Austernseitlings (*Pleurotus ostreatus*) und des Stockschwämmchens (*Pholiota mutabilis*), auf Laubholzstübben wieder aufgenommen und weiter ausgebaut (BAVENDAMM, WITT). Von besonderem Interesse sind auch die umfangreichen Pilzzuchtanlagen des Praktikers LUTHARDT in Steinach/Thür. Wald, der im Kriege ein besonderes Verfahren entdeckte, das Stockschwämmchen auf Buchenholz in wirtschaftliche Grosskultur zu nehmen und wertvolle Beobachtungen z. B. an Speisepilzrassen machte.

Das Problem der künstlichen Zucht von holz- und humusbewohnenden Speisepilzen steht einmal in Zusammenhang mit der Champignonzucht, da es sich bei der rentableren

Beetkultur und der in Deutschland in den Handel gebrachten Brut von Wildpilzen um ähnliche Substrate handelt, wie sie als Ersatz für den selten gewordenen Pferdedünger überall in grosser Zahl erprobt werden, zum anderen stellt es uns vor zahlreiche, noch nicht ausgeschöpfte wissenschaftliche Aufgaben, die auf dem Gebiet der Bodenkunde bzw. der Humusforschung, des Waldbaus und des Forstschutzes, der Lignin- und Zelluloseforschung u. dgl. liegen (MELIN, FRIES, LINDBERGER, LEACH, u. a.). Besonders unter den Humuspilzen kommen Arten vor, die dem Champignon an Wohlgeschmack nicht nachstehen und auch einen ähnlich hohen Eiweissgehalt haben, wie neuere deutsche Untersuchungen aus der Kriegszeit von SCHMIDT-BURGK bzw. LINTZEL zeigen. Z. T. sind sie schon in früheren Zeiten mit Erfolg gezüchtet worden (COSTANTIN, MATRUCHOT, BULLER, MOUNCE, FALCK u. a.). Auch die Kultur wilder Champignons, wie des Anis- oder Schafchampignons (*Psalliota arvensis*), etwa nach TRESCHOW auf Fichtennadelstreu oder auf Komposthaufen, sowie die von bestimmten Würzpilzen, dürfte aussichtsreich und nicht nur für gewerbliche Betriebe, sondern auch für jeden Gartenbesitzer u. dgl. wertvoll sein. Ganz besonders wichtig ist aber vermutlich die künstliche Zucht von Speisepilzen, die, wie z. B. *Clitocybe candida* (HOLLANDE) oder *Lactarius deliciosus* (WILLSTAEDT u. ZETTERBERG), Antibiotica enthalten. Neben einer Zucht der genannten Pilze nach Art des Champignons zur Ausnutzung bisher unwirtschaftlich verwendeter fester Abfälle der Land- und Forstwirtschaft (Hansschäben, Sägespäne u. dgl.) müsste auch der submersen Kultur des

Speisepilzmyzels in Flüssigkeiten nach dem Muster des Biosynverfahrens (PEUKERT) und der Nährhefeherstellung (FINK u. a.) Beachtung geschenkt werden.

Discussion

E. RENNERFELT: Professor BAVENDAMM hat in seinem Vortrag von der Einwirkung von Antibiotika bei *Clitocybe gigantea* z.B. auf Gräser, die davon getötet wurden, gesprochen. Ich habe in der Nähe von Hexenringen von *Clitocybe gigantea* ähnliche Beobachtungen gemacht, wobei sowohl junge Kiefern wie auch andere Pflanzen getötet wurden. Vielleicht kann dies auf Produktion von Blausäure zurückzuführen sein, die als direktes Gift auf die anderen Pflanzen wirkt.

E. BJÖRKMAN: Es ist sehr interessant zu hören, wie man die Fruchtkörper von holzerstörenden Pilzen verwenden kann. Ich will nun fragen, ob Sie der Meinung sind, dass man ligninzersetzende Pilze auch zur Vorbearbeitung des Holzes bei der Zellulosefabrikation verwenden könnte.

W. BAVENDAMM: Theoretisch ist das möglich, aber praktisch voraussichtlich nicht. Die Ligninspezialisten unter den Holzpilzen greifen zwar nach unseren bisherigen Kenntnissen, die allerdings gerade auf diesem Gebiet noch verhältnismässig gering sind, zuerst das Lignin an, aber doch auch sehr bald die Zellulose, so dass es schwer sein dürfte, eine eventuell eingeleitete künstliche Holzerstörung zur rechten Zeit abzubrechen. Es müsste ausserdem noch untersucht werden, ob sich alle Ligninzer-setzer gleich verhalten. Für wissenschaftliche Zwecke, d. h. für die Zellulose- und Ligninchemie, hat sich allerdings die Benutzung von Holzpilzen als sehr nützlich erwiesen.

E. BJÖRKMAN: Wir wissen, dass typische Fruchtkörper von *Lentinus lepideus* sich nur im Licht entwickeln. Kennt man eigentlich die Ursache dieses Phänomens?

W. BAVENDAMM: Es gibt verschiedene Holzpilze, die normale Fruchtkörper nur im Licht entwickeln, während andere das offenbar auch

im Dunkeln können. Die wirkliche Ursache dafür kenne ich nicht. Es müssen u. a. auch noch Versuche gemacht werden, ob vielleicht ein kurzer Belichtungsreiz genügt, um die Pilze zur Fruchtkörperbildung zu veranlassen.

W. P. K. FINDLAY and J. G. SAVORY
(Princes Risborough, Bucks.)

Breakdown of Timber in Water Cooling Towers

A review is given of records in the literature of breakdown of wood by fungi which preferentially attack the central layers of the secondary walls of wood elements, in timber in wet conditions. This type of breakdown may assume economic importance in industrial water cooling towers. The appearance of affected wooden slats from cooling towers and the unusual type of penetration of the cell walls therein are described. The water cooling tower is considered as an ecological unit. Methods of isolation of fungi from the affected wood are described and the fungi isolated listed. An account is given of a number of other situations in which a similar type of fungal attack has been observed.

Attempts to reproduce this type of breakdown in the laboratory are described.

The general conclusion is reached that, at present, there is no evidence to show that fungi of the types under discussion are primary agents in the breakdown of wood. Indications so far obtained suggest that their presence is secondary following upon partial decay by wood-destroying basidiomycetes or partial hydrolysis by water, heat, or chemicals.

Discussion

D. V. BAXTER: Rapidity of decay undoubtedly depends upon a number of factors, but I should like to inquire of Dr. FINDLAY as to the approximate shortest time this effect has been noticed.

W. P. K. FINDLAY: The life of timber slats in cooling towers may be 20 years, but failure

in 5 years has occurred. The length of life appears largely to depend on the quality of wood. Penetration of cell walls of the type described can occur in a few months in the laboratory.

W. W. VAROSSIEAU: I was very interested in Dr. FINDLAY's paper, especially as reference was made to ancient buried, water-saturated wood, decayed by fungi. My own investigations on pilings from the foundations of destroyed buildings at Rotterdam showed that in this material a decomposition of cellulose takes place without fungi being present. The difference might be caused by the absence of oxygen in the latter case. Bacteria proved to be present in the wood from the Rotterdam pilings, but it is not sure whether they play an active role in the cellulose decomposition or not.

E. RENNERFELT (Stockholm)

Heartwood Constituents in some Conifers and their Fungicidal Properties

During the last ten years comprehensive studies on the heartwood substances of conifers have been carried out under the guidance of professor ERDTMAN at the Royal Institute of Technology, Stockholm. These investigations have led to the discovery of several new natural compounds. Characteristic components of the heartwood of the genus *Pinus* are pinosylvin and pinosylvin monomethyl ether. They prevent the digestion of pine heartwood according to the normal sulfite method. Pine heartwoods also contain several other substances, part of which are characteristic for the *Haploxyton*-group. Thus, the occurrence or absence of heartwood components commands great interest in relation to taxonomy.

At the Forest Research Institute these substances have been tested regarding their toxicity against fungi. In decay experiments with pine heartwood it has been shown that as a rule the outer heartwood is more resistant than the inner, which conforms with observa-

tions with *Larix* and *Sequoia*. Some fungi do not attack the heartwood at all or only very slightly. Examples are *Coniophora puteana* and *Merulius lacrymans*. On the other hand *Poria vaporaria* and especially *Lentinus lepideus* decompose pine heartwood almost without difficulty.

In experiments with pure pinosylvin or pinosylvin monomethyl ether it was found that they are very effective against various fungi. The mycelium of *Coniophora* and *Merulius* is checked in a nutrient solution containing 0.002–0.005 per cent pinosylvin, and *Lentinus lepideus* and *Polyporus annosus* are checked in solutions containing 0.01–0.02 per cent pinosylvin. The germination of the *annosus*-conidia is checked in solutions containing as little as 25–50 p. p. m. of pinosylvin.

Thuja plicata, Western red cedar, possesses a very resistant heartwood. From this wood ERDTMAN and GRIPENBERG isolated three isomeric substances, α -, β - and γ -thujaplicin, which contain a novel ring system with seven carbon atoms. These substances are all very strong fungicides. Thus they check decay fungi in concentrations of 0.001–0.002 per cent. The germination of spores of blueing fungi was prevented in concentrations of 0.01–0.02 per cent. The toxicity of thujaplicin is of the same order as that of sodium pentachlorophenolate.

Discussion

W. P. K. FINDLAY: Has the occurrence and quantities of tannin and tannin like substances in coniferous wood been investigated?

E. RENNERFELT: Some coniferous wood, as for instance the *Sequoia* heartwood, contains a considerable amount of tannin, and the great durability of this wood possibly depends partly on this tannin content.

L. HUTCHINS: Is it possible to demonstrate the occurrence of these heartwood substances in young trees, or is it possible to prove precursors of them in the sapwood?

E. RENNERFELT: Generally, it is necessary to have trees with heartwood substances. In

the Scots pine, however, Professor ERDTMAN has succeeded in demonstrating small quantities of all heartwood constituents in the sapwood.

W. BAVENDAMM: Eignen sich nicht die *Sequoia*-Arten für solche Untersuchungen?

E. RENNERFELT: Neben Tannin sind mehrere krystalline Substanzen aus dem Kernholz von *Sequoia* isoliert worden. Sie sind aber nicht auf ihre fungizide Eigenschaften untersucht worden.

H. ROBAK: Is there a connection between site, climate, or other external factors and the content of pinosylvins in the trees?

E. RENNERFELT: Preliminary investigations seem to indicate that there is no such connection.

HELENE FRANCKE-GROSMANN (Reinbek/Hamburg)

Zur Ökologie und Taxonomie eines mit Borkenkäfern vergesellschafteten Bläuepilzes, Ophiostoma ips (Rumb.) Nannf.

Im Sachsenwald bei Hamburg tritt der Bläuepilz *Ophiostoma ips* mit dem grossen Kiefernborke n k ä f e r *Ips sexdentatus* BOERN. vergesellschaftet auf. Dieser Pilz hat die Eigenart, seine langhalsigen, meist zilienlosen Fruchtkörper nicht nur oberflächlich oder in Hohlräumen (Insektenfrassgängen), sondern auch völlig in das weiche Parenchym der inneren Rinde versenkt auszubilden. Die Rolle des Halses als Sporenträger wird dann hinfällig. Bereits in einem nur 2-3 Wochen alten Frassbilde des Käfers lassen sich die jungen Fruchtkörper von *O. ips* in der Nähe des Mutterganges feststellen, tief eingebettet in das der Nekrose verfallende Rindenparenchym, welches zwischen den einzelnen Larven g ä n g e n stehen bleibt. Die Jungkäfer fressen später beim Reifungsfrass diese von den Larven verschonten, von Fruchtkörpern und Sporen durchsetzten Rindenteile. Die klebrigen, durch eine Gallerthülle geschützten, fast vier-

kantig-prismatischen Sporen passieren ungeschädigt den Verdauungskanal des Käfers. Man darf wohl annehmen, dass die Eigenschaft des Pilzes, seine Fruchtkörper auch submers ausbilden zu können, eine Anpassung an endozoische Verbreitungsweise ist.

Der Pilz, welcher nach den Beschreibungen von RUMBOLD sowie von NISIKADO und YAMAUTI, aber auch durch Vergleich mit einer Originalkultur aus Baarn identifiziert werden konnte, ist von seiner Autorin als *Ceratostomella ips* beschrieben worden, da er in Nordamerika (und auch in Japan) als Begleiter verschiedener Ipsiden auftritt. Er wurde später von NANNFELDT zur Gattung *Ophiostoma* H. u. P. SYDOW gestellt, welche von ihm in die *Plectascales* eingereiht wurden, da nach den bis dahin vorliegenden Untersuchungen ihre Fruchtkörper ungeordnete Asci besitzen. Zu *Ophiostoma* rechnet NANNFELDT auch die Gattung *Endoconidiophora* MÜNCH, die jedoch von anderen Autoren, wie DAVIDSON, aufrecht erhalten wird. GÖDDANICH zählt den Pilz—sicherlich zu Unrecht—in seine Gattung *Gros-mannia*.

Entgegen den bisherigen Befunden stellte sich bei der Untersuchung der Fruchtkörper von *O. ips* in Quetsch- und Schnittpräparaten heraus, dass die keulenförmigen, gestielten, acht Sporen enthaltenden Schläuche büschelförmig angeordnet sind. Das Ascusbüschel befindet sich am Grunde des Fruchtkörpers, dem Ansatz des Halses gegenüber. Es entspringt einem etwa kegelförmigen Stratum fertiler Hyphen, dessen Rand mit den Wandungen des Fruchtkörpers in Verbindung steht. Die reifen Asci verfallen der Verschleimung.

Da dieses Ergebnis den bisherigen Befunden bei *Ophiostoma* widersprach, wurden mit den gleichen Methoden noch einige weitere *Ophiostoma*-Arten untersucht. Dabei konnte festgestellt werden, dass eine büschelige Anordnung der rundlichen oder keulenförmigen Asci bei der Gattung *Ophiostoma* weit verbreitet ist. Bei *Grosmannia penicillata* (GRSM.) GOID. scheinen die Schläuche unregelmässig angeordnet zu sein.

Eine Aufteilung der Gattung *Ophiostoma* sensu NANNFELDT zum mindesten in solche Arten mit büscheligen und solche mit regellos angeordneten Asci wird sich beim genaueren Studium der Fruchtkörper nicht umgehen lassen. Möglich, dass dabei auch die MÜNCHSche Gattung *Endoconidiophora* wieder allgemeine Anerkennung finden wird, was nicht verwunderlich wäre, da die endogene Sporenbildung und der eigenartige Estergeruch, welcher alle Angehörigen der Gattung auszuzeichnen scheint, auf eine andere Entwicklungsreihe hindeutet. Bedauerlich ist, dass die Typusart *Ceratostomella pilifera* WINT., auf welche die Gattung *Ophiostoma* gegründet wurde, nicht mehr mit Sicherheit feststellbar ist. Jedenfalls lässt sich die Gruppe der *Ophiostoma*-Arten mit büschelig angeordneten Schläuchen als einen Übergang zu den niederen *Ascohymeniales* auffassen. Ihre Fruchtkörper haben zweifellos gewisse Ähnlichkeit mit den Perithezien der Gattung *Chaetomium* KUNZE.

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- AINO MATHIESEN (Stockholm)
Die Insektenbläuen in Schweden
- Die Insektenbläue und Luftbläue des Nadelholzes werden von artlich verschiedenen Pilzen verursacht. Die Bläue, welche gleichzeitig mit den Borkenkäferangriffen auf frisch gefällten oder stehenden Stämmen auftritt, wird meist von den zu der Familie *Ophiostoma* gehörenden Pilzen verursacht. Die durch den Borkenkäfer verschleppten Bläuepilze sind gewissermassen spezifiziert: gewisse Käferarten sind immer assoziiert mit denselben Pilzarten, die selbst bei den unter fast gleichen Bedingungen lebenden Käfern, wie *Blastophagus minor* und *Ips acuminatus*, nicht verwechselt werden. Sowohl der Pilz als der Käfer können aber selbständig existieren und zur vollen Entwicklung gelangen. Neben solchen hoch spezialisierten Pilzformen gibt es andere, welche regelmässig zusammen mit mehreren Käferarten unter gleichen ökologischen Bedingungen auftreten und solche die sporadisch zusammen mit mehreren Käferarten vorkommen.
- In Schweden gehören zu den streng spezialisierten Formen Pilze, welche assoziiert mit *Blastophagus minor* auf Kiefer auftreten, eine intensive und schnell wachsende Bläue verursachend, nämlich *Ophiostoma canum* und *Trichosporium tingens*. *O. canum*, bisher nur auf dem von *Bl. minor* angegriffenen Holze gefunden, wird hauptsächlich durch die Graphien sporen verbreitet, welche dicht die Wände der Insekten- und Larvengänge bedecken. Die klebrigen Sporen werden von den Insekten innen- und aussenwendig getragen. Diesen Pilz findet man im Holze schon in der ersten Woche nach dem Anfluge. *Trichosporium tingens*, morphologisch und physiologisch von der ersten Art scharf verschieden, gehört zu den imperfekten Pilzen und wird ebenfalls in frühen Stadien des Angriffes gefunden. In Gängen mit abgestorbener Brut von *Bl. minor* findet man auch andere Bläuepilze, wie die Luftbläuen *O. coeruleum*, *O. piceae* u. a. selteneren Arten. Mit dem ebenfalls kiefern bewohnenden *I. acuminatus* ist stets eine bisher unbe-

schriebene *Ophiostoma*-Art, spezifisch für diesen Käfer, vergesellschaftet. Diese Art wird ebenfalls hauptsächlich durch die Konidienform verbreitet und bildet sehr selten Perithezien. Wahrscheinlich sekundär wird *O. pini* öfters zusammen mit *I. acuminatus* gefunden. *Pityogenes quadridens* trägt meist keine Bläuesporen mit sich. Auf Fichte ist *Ips typographus* ständig assoziiert mit *O. penicillatum*, einer polymorphen Art, welche jedoch auch mit anderen fichtenbewohnenden Borkenkäfern, wie *Hylurgops palliatus* und *P. chal-*

cographus auftreten kann. Auf alten Angriffen von *I. typographus* kommen *O. piceae* u. a. Luftbläuen hinzu, welche später überhand nehmen. *Hylurgops palliatus* trägt oft eine abweichende Form von *O. penicillatum* mit sich; *Pityogenes chalcographus* trägt meist keine Bläuen. Auch die Holzböcke werden assoziiert mit Bläuepilzen gefunden: in den Gängen von *Acanthocinus aedilis* wurde *O. olivacea* n. sp. gefunden und mit *Tetropium* sp. *O. tetropii* n. sp., eine schwache Bläue verursachend.

SESSION 8

July 20th, 9 a. m. — noon, Attendance: 35 members

Chairman: H. VAN VLOTEN, Recorder: E. BJÖRKMAN

SUBJECT:

Various Papers

D. V. BAXTER (Ann Arbor, Mich.) *Relation of Cultural Practices to Disease in American Forest Plantation*

The problems of disease prevention and control in artificially restocked stands include questions of planting methods, species used, site selection, and the type of cultural treatments applied. Many of the answers to these problems can be found in existing plantations.

Among the oldest plantations in the United States are those established between 1890 and 1911 on the Biltmore Estate, near Asheville, North Carolina. The "Pinetum" in the Lake States (East Lansing) was established in Michigan in 1896, and the Saginaw Forest Plantations (Ann Arbor) of white pine date back to 1904.

In all three of these historical plantations, early evidence of butt and root rot points to sources of considerable loss in stands planted on similar sites in the future. From the records of plantation disease, kept for the Pinetum and for Saginaw Forest, *Polyporus Schweinitzii* FR. will be a chief cause of root rot in

white pine in the Lake States. In the southeastern section of the United States, *Fomes annosus* FR., much as on European plantings, is the chief fungus involved, but *Pol. circinatus* FR. and *Pol. Schweinitzii* also cause some of the decay.

Most plantations are not old enough to be seriously affected by stem or "top" rots. *Robinia pseudacacia* which has been planted perhaps more widely than any hardwood species in America, has been infected with *Fomes rimosus* BERK., especially following severe attacks by the locust borer. The most serious stem rot in plantations on the continent has been experienced with *Shepherdia argentea* in shelterbelts in the short grass plains areas of the West. The decay is caused by *Fomes fraxinophilus Ellisianus* BAXTER. When planting experiments were begun on the Northern Great Plains, the buffalo berry was tested because the tree was one of the comparatively few native arborescent plants that appeared to survive drought. It has now been the experience that *Shepherdia argentea* in shelterbelts is so subject to breakage, and breakage

followed by heart rot, that extensive use of this tree is discouraged. The fungus may destroy shelterbelt plantings no older than twenty or twenty-five years.

Decay in the extensive plantations of *Pinus divaricata* on the Nebraska National Forest has followed sunscald and injury resulting from pruning operations. In the pines, rot occurs in the areas of conspicuous sunscald scars that resulted from pruning, and not at the cutting wounds. It is apparent that decay will finally lead to the destruction of many of these historical stands.

Lenzites saepiaria Fr. is at least one of the causes of rot in the standing trees. *Pinus ponderosa*, because of its thick bark, has not been damaged by sunscald as a result of pruning. Decay has not developed in near-by shelterbelt plantings of *Juniperus virginiana* and *J. scopulorum*, although these trees are subject to breakage from winter storms.

Certain rust fungi have become a serious obstacle to the successful growth of pine in American plantations. *Cronartium fusiforme* (A. & K.) HEDGC. & HUNT has become increasingly prevalent, partly because of widespread planting of *Pinus caribaea* on sites that formerly grew *Pinus palustris*. *Cronartium complanatum* ART. has restricted the planting of *ponderosa* pine in the Lake States to certain limited areas where *Myrica gale* does not grow. Control of *Cronartium ribicola* FISCHER is important but relatively simple.

Our experience to date with plantations in the United States shows clearly that if we are to be thoroughly successful, small unit planting is advisable. Furthermore, units should be planted "species wise" (to different species), not only using the kinds of trees adapted to the site, but also established with the knowledge and understanding of the conditions under which disease is likely to be a serious threat in forest practice.

Discussion

H. VAN VLOTEN: I thank Professor BAXTER, our president, for his important contribution.

The effect of cultural practices upon tree diseases is an outstanding problem for practical forestry. We cannot spend so much money by spraying or dusting and similar direct measures of treatment, as we are able to do economically in e.g. horticulture. This problem, therefore, is one of the points of our urgency program in Section 24 of the International Union of Forest Research Organizations.

H. HEIBERG: Which were the host plants for the rusts on slash pine and *Pinus ponderosa*?

D. V. BAXTER: *Cronartium complanatum* has restricted the planting of *Pinus ponderosa* in Michigan to areas where the alternate host, *Myrica gale*, does not grow. In the south, *Cronartium fusiforme* is a serious obstacle to successful growth of slash and loblolly pine plantations. The rust fungus infects the black oaks, and especially water oak, willow oak, and laurel oak.

L. HUTCHINS: What is your opinion, Dr. BAXTER, of plantation at Ann Arbor, Mich., of black walnut interplanted with black locust (*Robinia pseudacacia*)?

D. V. BAXTER: Plantations of *Juglans nigra* mixed with *Robinia pseudacacia* show much greater growth in height and diameter than the walnut planted in pure stands. This indicates that a more rapid growth of walnut takes place in plantations mixed with locust if the soil is lacking in nitrogen. Because of the rapid growth of the locust, the *Robinia* is cut back frequently, since it is kept solely to improve the soil. The locust will sprout again after cutting. Without this practice, the *Robinia* will whip the walnut. In regions subject to drought, locust should be used with care in mixed plantings. The locust is most apt to survive at the expense of the other tree in the mixed plantation during droughts.

E. BJÖRKMAN: It is very interesting that certain rot fungi of great practical importance in Sweden, in particular *Polyporus annosus*, seem to be rather rare in the United States. On the other hand fungi such as *Polyporus Schweinitzii*, occurring only sporadically in Scandinavia, are very common in America.

As to *Lenzites sepiaria*, which can occur as a parasite in living trees in the United States, the same fungus has only been found as a saprophyte in Sweden, at least as far as I know.

D. V. BAXTER: We do not understand why many forest fungi are abundant in European forests and are rare in America under site conditions that appear to be similar. Likewise, it is difficult to explain why certain common forest fungi in America are seldom found in Europe, even though they occur in both continents. Some fungi, however, seem to grow best in certain American forest regions because summer temperatures apparently favor their insect vectors.

H. VAN VLOTEN: Is it really true that rust (*Cronartium*) is more common in open stands, just because these are open, or are the stands open because of the rich occurrence of rust?

D. V. BAXTER: Mortality from trunk infection is known to be highest in the seedling-to-pole stages of the pine. Infected saplings are usually killed within a few years. This would make the stands more open. Older trees may live for a number of years, but break during storms at the canker so that the "opening up" of the stand continues. But the most significant factor involved in the prevalence of the rust is the presence of susceptible oaks. If pine and susceptible oaks are both abundant, much infection may usually be expected.

J. S. BOYCE (New Haven, Conn.) *Development of Tree Diseases in the United States*

Pathology of forest trees in the United States had first to concern itself largely with losses caused by decay in immense stands of overmature timber. In the West, the prevention and control of decay and the proper utilization of decayed wood is still of primary importance.

Douglas fir (*Pseudotsuga taxifolia*) is an example. More than one-fourth of all the

saw timber in the United States is Douglas fir in western Oregon and Washington. However, of this vast volume about 15 per cent on the average is now a loss from decay, with losses in individual stands amounting to 50 per cent or more. This decay is largely caused by *Fomes* (*Trametes*) *pini* with other fungi playing a lesser part. Investigation begun over thirty years ago was never completed because the information obtained was sufficient at the time, but with the depletion of timber resources and the great increase in values it is now inadequate. Research has begun again, not only by forest pathologists to determine under what conditions Douglas fir can be grown with the minimum of decay, but also by wood technologists and chemists to find uses for wood already decayed.

In the eastern United States with the removal of nearly all the virgin timber, emphasis shifted to diseases of younger stands. It is now apparent that many of the pathological difficulties that have been present in western Europe for so long and which seemed to be absent in the United States are now developing because conditions over limited forest areas in the East have become similar to those in Europe. For instance, some years ago following drought, a hitherto harmless fungus, *Tympanis pinastri*, attacked red pine (*Pinus resinosa*). The significant point was not the damage caused but the fact that the attack was confined to red pine outside its natural range. *Fomes annosus*, which has been well known in the United States for a long time as relatively harmless, is becoming increasingly damaging to conifers such as red pine, eastern white pine (*Pinus strobus*), red spruce (*Picea rubra*), and others, either in plantations where the trees are outside their natural range or on unsuitable sites, and in stands of unnatural composition, i.e. pure stands when the usual habitat of the tree is in mixture. Thus, developments in the United States are analogous to those in Europe, but our difficulties may never be as serious as in Europe since it is hoped to avoid widespread establishment of

artificial stands and to retain the stand composition that nature has evolved through the ages.

Finally, a new type of disease is appearing in American forests. For decades European literature has discussed the dying of spruce, silver fir, larch, and oak. The causes seemed most controversial, but time has shown that basically the trouble has been the marked changes in forest conditions in Europe brought about by man, changes which developed for decades before the effects became apparent. The same situation is now faced in the United States with littleleaf disease of certain southern pines, dieback of birch, and pole blight of western white pine, the causes of which are baffling and obscure, but fundamentally probably originate in unnatural conditions. A long period of investigation will be needed to ascertain the cause and control of these diseases. These investigations should be facilitated by European experience and knowledge.

The paper was read by J. T. MIDDLETON.

Discussion

H. VAN VLOTEN: I wish to express our gratitude to Dr. MIDDLETON for reading this paper. But we regret very much that Professor BOYCE is not joining this meeting. He visited Europe three times in 1925, 1939 and 1950. He has been able to follow the development of tree diseases in the different European countries and his knowledge would have contributed very much to our discussions. His paper surely is another proof of the urgent need and usefulness of international cooperation.

D. V. BAXTER: Dr. BOYCE mentioned the importance of satisfactory utilization of decayed wood. It will be appreciated if Dr. BJÖRCKMAN will kindly inform the section about what is being accomplished in this field in Sweden.

E. BJÖRCKMAN: The results of my experimental work regarding the fitness of wood, damaged by different decay fungi, for pulping purposes, were published as No. 4 of Bulletins

from the Royal School of Forestry, Stockholm, Sweden, in 1949.

M. K. NOBLES: One company in British Columbia is producing decorative plywood using *Pseudotsuga taxifolia* decayed by *Fomes pini*. — Forest Products Laboratory has inquired what fungus could be used to produce brown cubical decay in wood since a certain percentage of such decayed wood was required for certain wallboard formula.

A. J. RIKER, T. F. KOUBA, W. H. BRENER, and R. F. PATTON (Madison, Wis.)

White-Pine Trees Selected for Resistance to White-Pine Blister Rust

To secure white pine (*Pinus strobus* L.) resistant to blister rust (*Cronartium ribicola* FISCHER), some 150 trees were selected in Wisconsin in 1938 and 1939 which had withstood for over 15 years natural inoculation from nearby wild ribes. These bushes averaged between 10,000 and 65,000 feet of ribes live stem per acre. Rust was plentiful. Open pollinated seed was collected and veneer grafts were made from each tree.

Over 1,000 grafts and 10,000 seedlings were grown and planted in 4 × 12 foot beds with four replications at a rust nursery in central Wisconsin. Commercial seedlings were planted also. *Ribes cynosbati* L., *R. missouriense* NUTT., and *R. nigrum* L. were planted between each of the beds so that no tree was more than 6 feet from a ribes bush. The soil was fertilized and watered to induce vigorous pine growth.

Further rust inoculations were applied to one-half of the trees by fastening a telia-bearing ribes leaf to a top branch. Then each bed was covered with a muslin cage and kept moist at a suitable temperature for 60 hours. After this severe inoculation, over 99 per cent of the commercial seedlings died within 3 years.

Following this same treatment the parent trees (as grafts) in the nursery showed more

or less resistance; about 20 per cent showed high resistance. Such resistance appeared in one or more of these ways: (1) all needle lesions were less than 1/2 mm across; (2) stem infections either were negative or were greatly reduced in number and size; (3) stem lesions were corked out; (4) lateral stem lesions progressed so slowly that they failed to reach the main stem, only a few inches away, before the twig died; (5) cankers progressed slowly and failed to form aecia.

Almost all of the seedlings became infected, whether they were from commercial seed or from these selected trees.

With only natural inoculation, relatively few grafted trees became infected, but the commercial seedlings within 7 years became infected as high as 71 per cent. However, when the open-pollinated progeny of the most resistant trees were considered, the per cent that survived was significantly better than that of the controls.

Relatively inexpensive methods for vegetative propagation of the best trees seem possible.

The paper was read by L. HUTCHINS.

Discussion

D. V. BAXTER: These investigations by Dr. RIKER and his associates concerning resistant white pine have led to some of the most important contributions made to forestry in the Region of the Great Lakes.

H. HEIBERG: Dr. HEIMBURGER, Southern Exp. Station, Maple, Ontario, even works on breeding of resistant white pine along the same line as Dr. Riker. He told a visiting Norwegian forestry expert that he had great success with his grafts, and one of the tricks

was to store the scions in cold water—mixed with ice—for 14 days before grafting.

H. ROBAK: Do you not have to use propagation by seed with extensive reforestation, because of the dangers involved when using clones?

H. VAN VLOTEN: I want to thank Dr. HUTCHINS very much for the reading of this paper. The research is of the greatest interest and I am glad to have been able to listen to it in detail. One question seems to be important. Could Dr. HUTCHINS tell us whether the resistant individuals are considered as the "end and purpose" of the experiments, or are they "starting points" for further breeding work? Is the idea to propagate the resistant individuals on a big scale to use them in practice, or will they be used in seed-orchards as mother trees?—I like to warn you not to rely on one or a few clones only (remember the Dutch elm tree in the Netherlands). If any other cause might appear sometime, all your selected trees might be wiped out.

L. HUTCHINS: These questions are very pertinent. When we began the work the first step was to establish whether or not we could secure white pine resistant to blister rust. Now that we have such trees, we are using them for further work. This includes (1) cross pollination of resistant trees, (2) vegetative propagation by grafting to establish seed orchards, and (3) experiments to root cuttings for reforestation work. Progress has been made already.—We are particularly concerned about having a number of different clones. So far 3 dozen of our selections have real promise. However, we are attempting to find even more not only with rust resistance but also with other elite characteristics.

GENETICS, GEN

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Vice-Recorder: A. GUSTAFSSON

SESSION 1

Jointly with Section CYT: July 12th, 2—4 p. m.

Chairmen: Ö. WINGE and C. D. DARLINGTON

SUBJECT:

Introductory Meeting

A. F. BLAKESLEE (Northampton, Mass.)
*New Hybrids in Datura from Culture of
Excised Embryos*

The Smith College Genetics Experiment Station has been making a study of the barriers to crossability between species. One of the most important barriers in *Datura* is inhibition of growth of hybrid embryos which have developed from species crosses. Of the 90 theoretically possible hybrids between the 10 *Datura* species, only 19 have been secured from viable seeds. Bursting or slow growth in a foreign style may prevent pollen tubes from reaching the ovules, especially when a long-flowered is pollinated by a short-flowered species. Failure of fertilization, however, appears not to be a barrier in *Datura* since in all cases in which the sperms reached the egg cells, fusion has resulted. Inhibition may occur at different stages of development of the hybrid embryos. Through techniques developed by VAN OVERBEEK and CONKLIN, arrested embryos may be excised and cultivated in artificial media. By this procedure 30 new

Datura hybrids have been secured which were not otherwise possible. For culture of the younger embryos, coconut milk or malt extract in the medium was found a useful stimulator. A method of "micrografting" has been developed to secure continued growth of cultured embryos which sometimes produce shoots without roots. The barrier of slow-growing pollen tubes has been overcome in some cases by style splicing. Drs. SATINA and RAPPAPORT have shown that embryo inhibition is caused by ovular tumors which in incompatible crosses develop from the single-layered endothelium surrounding the embryo sac which normally functions as nurse cells. Extracts from ovular tumors contain a thermostable substance unrelated to plant hormones which inhibits normal embryos both *in vitro* and *in vivo*. The inhibiting potency is retained through at least 4 passages of injection into young capsules suggesting a self-duplication or a new formation of the inhibitor stimulated by the originally injected ovular tumor extract. Ultra violet absorption spectra indicate that the inhibitor is related to nucleo-

proteins. Attempts to neutralize or otherwise inhibit the activity of the inhibitor if successful might greatly increase the number of wide species crosses possible and enable the plant breeder to develop new pure-breeding types with hybrid vigor through doubling by means of colchicine the chromosome number of the sterile hybrids thus secured.

D. CATCHESIDE (Cambridge)

The Nature of Gene Mutations

Knowledge of the composition of the gene is still in an elementary state. It is usual to suppose that genes are large nucleoprotein molecules, but whether the specificity resides in the compound as a whole or in one of the components and whether in surface configuration or elsewhere, are matters of conjecture. Certainly we are far from the state of having pure preparations of a wild type gene and of one of its mutants to compare. Information about the gene, upon which theories may be based, is indirect and derived from its second and third order reactions, its physiological and biochemical activities and by what alterations occur when a gene alters.

It is improbable that a gene intervenes directly in the physiological reactions it controls, but rather that it produces entities which are either the enzymes directly concerned in metabolism, or their precursors or progenitors. Mutants might be expected either not to produce the specific enzyme or to produce an enzyme with the same specificity but with an altered degree of activity or stability. The latter might spring from altered physicochemical properties, such that the enzyme is more sensitive to inactivation either by extra- or intracellular agencies. Thus glutamic dehydrogenase is absent from a mutant unable to aminate α -ketoglutaric acid. Pantothenic desmolase is present in a mutant unable to condense β -alanine and pantoyl lactone, but inactive in intact cells, though active in cell-free homogenates. Tryptophane desmolase may be present in altered form in a mutant unable

to condense indole and serine. The enzyme is inactive in intact cells and in crude extracts of them, but is said to be active in some purified extracts in which some properties appear to be different from those of the enzyme of the wild type.

In several instances, biochemical mutants require the growth factor only under certain conditions of growth, as in the temperature sensitive mutants which will grow without any supplement except at the higher part of the range of temperatures at which the wild type will grow. There are totally inactive alleles of some of these temperature sensitive mutants, showing that the partial activity of the latter can hardly be due to an alternative pathway for synthesis. The mutant differences appear to lie in differences in stability of the enzyme products of the allelic genes. The mutant allele differs from the normal in such a way that although it produces an enzyme with the same specificities, there are internal differences which lead to more rapid inactivation of the enzyme under conditions, such as higher temperature, in which the normal enzyme is nearly stable. This might theoretically be obtained by breaking certain hydrogen bonds of the protein molecule, so giving altered physical properties without altering, under some conditions, the spatial configuration that confers specificity. The spatial configuration would change under other conditions so that the molecule would fold and collapse into an inert protein lacking the surface specificity. The gene itself is protected from this configurational collapse.

Alterations in the cellular, as well as the external, environment would be expected to affect the stability of the gene products. Genetic changes of this character are perhaps exemplified by those suppressor mutants which, in the presence of an inactive mutant, remove either completely or partially the requirement of a supplement for growth of the mutant. In some cases there is evidence that suppressors may be non-specific in their activities, in that they promote a change in cellular

environment that has the effect of suppressing the characters of two or more unrelated gene mutants.

R. O. ERICKSON and M. OGUR

(Philadelphia, Penn.)

Nucleic Acids and Cell Division

Nucleic acid determinations have been made of developing microsporocytes, microspores and pollen grains of *Lilium longiflorum*. Previous studies of developing flower buds (ERICKSON, Amer. Jour. Bot., 35: 729) have shown that their growth in length is exponential; hence, log length of a flower bud serves as an index of its developmental status. Meiosis, microspore mitosis and anthesis have been located at definite points along the bud length axis. Anthers were dissected from buds of known length, and cell suspensions prepared from their contents. Cell counts were made of these suspensions, and they were analyzed for pentose nucleic acid (PNA) and desoxypentose nucleic acid (DNA) by the method of OGUR and ROSEN (Arch. Biochem., 25: 212). Analytical results were calculated to nucleic

acid, content in $\mu\text{g.}$ per microsporocyte, microspore or pollen grain, and plotted against log flower bud length.

DNA content per cell drops sharply at the end of meiosis, with the formation of four microspores from each microsporocyte. It then doubles gradually during the microspore interphase between meiosis and the microspore mitosis. At the time of microspore mitosis DNA content doubles rapidly. In the development of the resulting two-celled pollen grain, from microspore mitosis until opening of the flower, there is a further gradual increase of DNA content. PNA content of these cells follows the same pattern up to microspore mitosis at a level about twice that of DNA, increases sharply at mitosis, and continues to increase at a rate nine times that for DNA in the maturing pollen grain.

The absolute amounts of DNA and PNA are great. At the time of anthesis the two-celled pollen grain contains about 375 $\mu\text{g.}$ of DNA and 1705 $\mu\text{g.}$ of PNA.

(A full account has appeared in Experimental Cell Research, 2: 73-89, 1951.)

The paper was read by D. R. GODDARD.

SESSION 2

Jointly with Section EXT: July 14th, 9 a. m.—1 p. m.

Chairman: D. D. KECK

SUBJECT:

Occurrence and Causes of Apomixis in Nature

R. C. ROLLINS (Cambridge, Mass.)

The Nature and Occurrence of Apomixis in Parthenium (Compositae)

Seed production without fertilization and zygote formation is probably much commoner in the Angiosperms than is at present realized. An awareness by investigators of this probability is necessary to make known the full

extent and importance of apomixis. Furthermore, the usual cytological and embryological techniques should be complemented by controlled genetic experiments that would positively identify cases of pseudogamy and provide other sound information about apomixis.

Two species of *Parthenium*, *P. argentatum* and *P. incanum*, show facultative apomixis. Five other species of *Parthenium* reproduce

only by amphimixis. All of the populations of *P. incanum* studied, including those from stations in Arizona, New Mexico, Texas and Mexico, were found to reproduce by facultative apomixis. A different situation prevails in *P. argentatum*, where the presumed diploid with $2n=36$ chromosomes is amphimictic, while all of the polyploid forms are facultatively apomictic. The diploid amphimictic phase of this species is localized in north-eastern Durango, Mexico. The polyploid apomictic phases are widespread, extending from San Luis Potosi, Mexico, to Texas.

Parthenium argentatum and *P. incanum* hybridize at many points of contact in their ranges. Hybridization appears to be most prevalent where apomixis and polyploidy occur. In these areas, introgression is a common phenomenon. The combined effects of hybridization, polyploidy and apomixis has resulted in many distinguishable, relatively stable populations of both species. It is particularly notable in *P. argentatum* that dozens or even hundreds of different apomictic populations could be readily distinguished. These distinctive populations are comparable to the microspecies being set up by taxonomists in such genera as *Crataegus*, *Rubus*, *Hieracium*, and *Taraxacum*. These populations are not species, as can be readily shown by comparative studies between them and other species of *Parthenium* not showing apomixis. By selecting clearly defined species within a genus as standards of comparison, the taxonomist should not be misled into describing apomictic populations as species and thus obscure their true relationships to the species of which they are a part.

Discussion

J. L. CROSBY: If, over the ranges where *P. argentatum* and *P. incanum* overlap, there are differences in the extent to which they will hybridize, one would expect to find corresponding differences in the extent of apomixis. Where there is much hybridization, one would expect most apomixis, because then

apomixis would have greater selective advantage as an isolating mechanism.

Å. GUSTAFSSON: Is polyploidy present in those species too, in addition to *P. argentatum* and *incanum*, where the occurrence of apomixis is suggested?

R. ROLLINS: In *Parthenium confertum*, the species referred to in my paper, there is polyploidy present.

A. MÜNTZING: The conditions in the apomictic *Parthenium* species are in several respects closely similar to those in certain partially apomictic groups of the genus *Potentilla*.

E. ÅKERBERG (Uppsala)

The Progeny of Artificial Hybrids between Poa Pratensis L. (coll.) and Poa alpina L.

From the cross between *Poa pratensis* L. (coll.) and *P. alpina* L. (see ÅKERBERG, 1942) nine hybrid plants have been studied, five obtained after apomictic types of the species, which have aposporous and diplosporous embryo-sac formation, respectively, and four after a cross between sexual *pratensis* and apomictic *alpina*.

A. Apomictic *Poa pratensis* × apomictic *P. alpina*.

Of the five hybrid plants two were diploid hybrids ($2n=41$ and 45) and three triploid hybrids ($2n=69$, 95 and 102).

To judge from the characters of the F_2 -plants (morphology, embryology and chromosome number) four of the five plants must have had mainly sexual seed formation. The fifth plant ($2n=102$) seems to have a predominantly apomictic seed development.

In F_2 there was a segregation in different characters, of which the heredity has been controlled in 21 F_3 -families and 3 F_4 -families. In regard to the seed formation in F_2 the following types have been obtained.

1) Fertilization of reduced egg-cells (5 F_2 -plants). Aposporous cells have been observed in some F_3 -plants. In the progeny of one of these F_2 -plants a subhaploid plant with

$2n=16$ was found. It was quite similar to *Poa trivialis*, just as another subhaploid plant found by KIELLANDER (1942).

2) Fertilization of unreduced egg-cells. The unreduced egg-cells have arisen from aposporous cells (2 F_2 -plants). Hyperaberrants are formed with the chromosome number so far raised to $2n=144$.

3) Development of the unreduced egg-cell without its being fertilized (apospory followed by parthenogenesis, 11 F_2 -plants, two of which were rather uncertain).

4) Male parthenogenesis (3 F_2 -plants, all from the same F_1 -plant).

The number of families within the four groups is of course no expression in figures of the segregation. To be able to state this the zygote lethality must also be noticed, which may be especially great in plants belonging to group 1. The segregation of the seed formation seems also to be different in different hybrid plants.

In the embryological examination of F_1 - and F_2 -plants no case of diplospory has been observed.

The results seem to confirm the opinion of MÜNTZING that apomixis is due to a delicate genetic balance, and of POWERS and others that the inheritance of apomixis involves three major steps—1) failure of reduction of number of chromosomes, 2) failure of fertilization, 3) development of the egg-cell into a new individual without its being fertilized.

B. Sexual *Poa pratensis* × apomictic *P. alpina*.

All the four hybrid plants were diploid hybrids and they showed a very great segregation in F_2 . The same is the case in five of the six studied F_3 -families. (The sixth family is too uncertain to be discussed.) One would have expected that the chromosome numbers of the F_3 -family would be just about the same as in the hybrid plants (where the number ranged between 66 and 70). Two of the families seem to have been developed from F_2 -plants, arisen from fertilization of unreduced egg-cells. It may be that gamete lethality gives an increased chance for the new aposporous cells,

which are developed in these hybrid plants. In the used mother-plant of *Poa pratensis* a tendency to apospory has also been shown.

A more detailed report will be published in *Hereditas*.

Literature

- KIELLANDER, C. L. 1942. A subhaploid *Poa pratensis* L. with 18 chromosomes and its progeny. *Sv. Bot. Tidskr.* 36: 200–220.
 MÜNTZING, A. 1940. Further studies on apomixis and sexuality in *Poa*. *Hereditas* 17: 131–153.
 POWERS, L. 1945. Fertilization without reduction in guayule (*Parthenium argentatum* Gray) and a hypothesis as to the evolution of apomixis and polyploidy. *Genetics* 30: 323–346.
 ÅKERBERG, E. 1942. Cytogenetic studies in *Poa pratensis* and its hybrid with *Poa alpina*. *Hereditas* 28: 1–126.

Discussion

C. L. KIELLANDER: In the F_1 – F_3 of that subhaploid triplet of *Poa pratensis* ($2n=\pm 72$), which had $2n=18$ and—as described by me in 1942—was similar to *Poa trivialis*, there is a high variation in chromosome number. There are many plants with $2n=15$ and at least two plants with $2n=14$. I wish to take this opportunity to mention this, because together with the now reported finding of a new subhaploid *Poa pratensis* twin with $2n=16$, which is also quite similar to *Poa trivialis* ($2n=14$), it must be considered a definite proof that *Poa trivialis* has taken part in the origin of *Poa pratensis*.

A. RUTISHAUSER (Schaffhausen)

Sexuality and Apospory in Some Pseudogamous Plants

Pseudogamous species combine qualities of apomictic and sexual plants: their unreduced egg-cells are able to divide without fertilization; but seeds capable of germination only result if flowers have been previously pollinated.

It is probable that pollen acts indirectly, by way of the endosperm, on the development of

the seeds. As GUSTAFSSON and GENTSCHOFF have shown, the endosperm of pseudogamous *Potentilla* itself is stimulated to develop by fertilization of the sec. embryosac nucleus. We have now demonstrated that, contrary to earlier findings, in pseudogamous microspecies of *Ranunculus auricomus* and *R. cassubicus* the central cell is, as a rule, also fertilized; the number of chromosomes at endosperm mitosis in two such forms, e.g. *R. argoviensis* ($2n=32$), amounts to 80; other forms, e.g. *R. puberulus* ($2n=32$), develop endosperm tissues with 80 or 96 chromosomes. In two cases we found 32 and 64 chromosomes.

With many *Potentillas*, not only the central cell but also the egg-cell shows a certain tendency to sexuality. Although most of the plants used in our experiments are completely aposporous (i.e. they produce only unreduced embryosacs), they were able—with a few exceptions only—to produce sporadic “triploid” hybrids. The degree of sexuality depends on both seed-plant and pollen-plant.

With *Potentilla* the tendency to apospory varies slightly. A change of this characteristic has so far been observed to occur only after genomes of a different species or strain have been introduced by crossing. Hybrids between parents partly pseudogamous and completely or to a high degree aposporous are indeed for the most part completely or to a high degree aposporous themselves, but in some of them the degree of apospory falls to 50% or 8% as the case may be. In our experiments there was no marked decline in apospory except where the parents differed from each other in their type of apospory.

We have succeeded in restoring pseudogamy and apospory by backcrossing the sexual specific hybrid *P. canescens* \times *verna* with either of the parental species, which were found to be pseudogamous, or by crossing it with related pseudogamous species. Backcrossed with the generative aposporous pollen-plant *P. verna*, *P. canescens* \times *verna* developed progeny partly sexual, not aposporous, but partly also pseudogamous or at least aposporous. In

their type of apospory the progeny correspond to a high degree with the pollen-plant; they are of generative aposporous type. Crossing with *P. argentea*, the somatic aposporous species used in our experiments produced, on the other hand, a somatic aposporous hybrid.

Discussion

A. MÜNTZING: Congratulations on the new technique which makes it possible to make accurate chromosome counts in the endosperm. This will greatly favour further work on apomixis in *Potentilla*.

H. G. BAKER (Leeds)

The Agamic Complex in Limonium (Sections Densiflorae and Dissitiflorae Boiss.)

Most species of *Limonium* are dimorphic in respect of pollen- and stigma-morphology. Type A pollen is accompanied by ‘cob’ stigmata and Type B pollen by ‘papillate’ stigmata. The two kinds of plant are self-incompatible but cross-compatible. Therefore, the regular occurrence of only one of the known self-incompatible types in a species, together with irregular pollen-formation or even complete male-sterility yet good seed-formation suggests the occurrence of apomixis. This has been proved wherever experiment has been possible. A preliminary report on these experiments, together with field- and herbarium-studies, is now permissible.

In the Densiflorae, *Limonium Durieui* KUNTZE (restricted to Algeria) and *L. ovalifolium* KUNTZE (which reaches from North Africa to Macaronesia and also along the coasts of western Europe) are dimorphic and apparently completely sexual. *L. densiflorum* KUNTZE appears to contain dimorphic and monomorphic (apparently apomictic) populations. *L. binervosum* C. E. S. ranges from Morocco to Scotland and northern Ireland and appears still to be spreading. It is tetraploid ($2n=32$) and all populations have cob stigmata. Apomixis in this species has been proved by continual emasculation, as it has in

'*L. transwallianum* PUGSL.' which is also a tetraploid and included within *binervosum* along with the other 'British endemics' ('*L. recurvum* C. E. S.' and '*L. paradoxum* PUGSL.') which appear to be of recent origin and are unlikely to be glacial relics. *L. binervosum* in certain regions is entirely male-sterile; nevertheless apomixis may be facultative for the species appears to be involved in the formation of natural hybrids.

L. lychnidifolium KUNTZE is triploid in the Channel Isles. The several 'varieties' of this species show different pollen and stigma combinations but each is monomorphic and apomixis has been proved in material from Jersey. Additional apparent apomicts are *L. Dufourii*, *L. Dodartii*, *L. Gougetianum*, *L. companyonis* and *L. Girardianum* (all names due to KUNTZE) while the monomorphic *L. confusum* KUNTZE is probably best placed in this section.

In the *Dissitiflorae*, dimorphic, presumably sexual species outnumber the monomorphics and are generally distributed about the Mediterranean. They include *L. spatulatum*, *L. Sieberi*, *L. graecum*, *L. psilocladon*, *L. duriusculum* and *L. minutiflorum* (all KUNTZE) in addition to '*Statice remotispicula*' LACAITA. *L. delicatulum* KUNTZE is monomorphic and probably apomictic as is *L. salsuginosum* KUNTZE and '*Statice inarimensis* GUSS.' The last-named should not be submerged under

the sexual *L. minutiflorum* as is current practice. *L. ocyimifolium* KUNTZE may be apomictic and may be better placed here than in the *Densiflorae*.

The assistance to taxonomy of these studies was discussed.

Discussion

D. H. VALENTINE: Are there any monomorphic self-compatible species in *Limonium*?

H. G. BAKER: Self-compatible species do occur in other sections of *Limonium* but these are cross-over types usually with Type A pollen and papillate stigmata.

N. W. SIMMONDS: Is apomixis in *Limonium* associated with notable phenotype and chromosome number variation?

H. G. BAKER: Populations of the apomictic species usually show intra-population uniformity but often considerable inter-population variability. No evidence of variation in chromosome number has been obtained.

G. F. L. TISCHLER: Is the basic chromosome number in this section 8 or 9? In *L. vulgare* both these numbers have been reported by different authors.

H. G. BAKER: Both 8 and 9 are basic numbers in *Limonium*. *L. vulgare* is a tetraploid on 8 (and is dimorphic), *L. humile* is a tetraploid on 9 (according to CHOUDHURI) and is monomorphic and self-compatible.

SESSION 3

Jointly with Sections CYT, EXT and TPH: July 14th, 2-5 p. m.

Chairmen: E. SCHIEMANN and L. F. RANDOLPH

SUBJECT:

Induced and Natural Polyploidy

G. TISCHLER (Kiel)

Über die Unterschiede der induzierten und natürlichen Polyploidien und ihre Auswirkung auf pflanzengeographische Probleme

Bei künstlichen Autopolyploidien vergrößern sich Kerne, Zellen und Organe: es entstehen

Riesenformen. Das Entwicklungstempo verlangsamt sich, und damit wächst die Neigung zum Perennieren. Der Gesamtstoffwechsel ist verlangsamt, der Wassergehalt der Zellen steigt, ihr Saugwert sinkt. Empfindlichkeit gegen tiefe Temperaturen und andere Schädigungsfaktoren nimmt zu. Positive Selektion.

tionscharaktere sind Vermehrung von Alkaloiden und ätherischen Ölen. Bezüglich Vitaminzunahme fehlt Übereinstimmung. Die Fertilität ist durch Störungen der Meiose geschwächt, ausser wo mit Polyploidisierung Selbststerilität aufgehoben wurde. Möglichkeit vegetativer Vermehrung ist von Vorteil.

Bei künstlichen Allopolyploiden wirkt die starke Steigerung der Variabilität ökologisch günstig. Natürliche Polyploide sind nur selten reine Autopolyploide. Riesenwuchs fehlt bei ihnen häufig. Die Geminibindung begünstigt volle Fertilität. Allmähliche Angleichung der künstlichen und natürlichen Polyploiden wird auf dem von v. WETTSTEIN durch Studien an *Bryum* und *Arenaria* gewiesenen Weg liegen. Veränderung der Kernplasmarelation dürfte der entscheidende Grund sein. Zu fordern sind vergleichende Chromosomen- und Kernmessungen. Mit veränderter Kernplasmarelation kann der Saugwert der Zelle zunehmen. Neigung zum Perennieren und zur Apomixis begünstigt Vordringen in schwieriger zu besiedelnde Biotope.

Mit der Variabilitätszunahme steigt die Zahl der für die Selektion nötigen Oekotypen. Die Regel, dass in Europa von Süd nach Nord die Polyploiden zunehmen, gilt selbst für Familien, die allgemein als hochpolyploid angesehen werden, wie die Gramineen. In Gesamtheit sind diese zu 60–70 % polyploid (Die Zählungen variieren etwas), auf den Kykladen zu 47 %, in Spitzbergen zu 95,2 %. Die gesamten Monokotylen haben auf den Kykladen 45,8 %, in Spitzbergen 97 % Polyploide. Für die Dikotylen gelten entsprechend 32,8 und 67,1 %, für die Gesamtangiospermen 35,5 und 76,9 %.

In der alpinen Flora ist die Ausmerzung der Diploiden viel geringer, da diese infolge eisfreier Kleingebiete nie ganz vernichtet wurden. Sie hatten Ausweichmöglichkeiten wie die Arten Nordamerikas oder Japans bei ihrer durch das Eisvordringen bedingten Südwanderung.

In den gemässigten Zonen können gleichfalls einige Biotope besonders reich an Polyploiden sein. Hierher gehören namentlich die Sumpfbgebiete. Umgekehrt gibt es eine Menge

Beispiele, bei denen mit Erhöhung des Polyploidiegrades die Xerophilie wächst. Die Ursache dieser Diskrepanz ist unbekannt. Ich vermute, sie wird in der Abnahme oder Zunahme der osmotischen Werte liegen. Auch hier fehlen exakte Untersuchungen.

In einigen Fällen spielt das Licht die Hauptrolle für den Übergang der Polyploiden in ein anderes Biotop. Die Bedeutung der Photoperiodizität ist umstritten.

Die Unkrautflora besteht in Mitteleuropa zum grossen Teil aus Polyploiden. Auch bei der Besiedlung der "Trümmerstätten" überwiegen die Polyploiden. Zufallserfahrungen mit diploiden und polyploiden Rassen von *Veronica* im Kieler botanischen Garten zeigten, dass unter ungünstigen Kulturbedingungen nur die Polyploiden übrig geblieben waren.

Discussion

T. DIANNELIDIS: Chromosomenzahlen an Pflanzen aus den Kykladen sind bis jetzt nicht untersucht worden. Deshalb haben die Angaben Tischlers über diploide und polyploide Pflanzen an den Kykladen, analogieweise aufgestellt, nur theoretischen Sinn. Die Pflanzen Südeuropas sind allgemein cytologisch wenig untersucht worden.

H. W. HOWARD (Cambridge)

Induced and Natural Polyploidy in Nasturtium and Rorippa

The work on *Nasturtium officinale* (watercress) has been published (HOWARD and MANTON, Anns. Bot., Lond., N.S. 10, 1–13 (1946) and HOWARD, J. Genet. 48, 111–18 (1947)), but there are three points which are worthy of further consideration. First it is suggested that the method used by HOWARD and MANTON to demonstrate the allotetraploid constitution of the wild tetraploid watercress should be very useful in other cases where diploid and tetraploid forms have been found in what has been considered a single species. The method consists of making an autotetra-

ploid by colchicine treatment of the diploid and crossing this autotetraploid with the naturally-occurring tetraploid. Studies of meiosis in the hybrid tetraploid obtained from this cross provide a means of deciding whether the naturally-occurring tetraploid is an allo- or an autotetraploid. Thus the hybrid tetraploid in watercress forms about 8 trivalents, 8 bivalents and 24 univalents per nucleus. This clearly shows that the naturally-occurring tetraploid is an allotetraploid. Secondly it is suggested that tetraploid species may sometimes initially be at a disadvantage compared with diploids due to a disturbed nuclear surface: cell volume ratio, and may evolve so as to resemble diploids in their "physiology." Thirdly there is the controversial question of nomenclature. HOWARD and MANTON made a new species, *N. uniseriatum*, for the tetraploid form of watercress, but AIRY SHAW has shown that there were prior specific names for it. One of these, *N. microphyllum*, has been accepted by myself (see HOWARD & LYON, *Watsonia*, 1, 228-33 (1950)), as very likely but there are difficulties in the original description (in particular "fructus Nasturtii brevis" which still seems to me to indicate very strongly the triploid hybrid and not the tetraploid species which has a long fruit). The rule of priority must be applied to nomenclatural problems if we are to avoid absolute confusion, but I would suggest that it should also be considered if previous systematists have really proved their case before accepting their name.

Three species of *Rorippa* are native of the British Isles. *R. sylvestris* is a hexaploid ($2n=48$). *R. islandica* is a tetraploid ($2n=32$), but a diploid form probably also exists. *R. amphibia* has both diploid ($2n=16$) and tetraploid ($2n=32$) forms. The tetraploid is probably an allotetraploid and it is proposed to confirm this by the same method as used for *N. microphyllum*. These results for *R. islandica* and *R. amphibia* suggest that there still must be many so-called species in which diploid and tetraploid forms exist and in which the two forms will not be found so long as

botanists are content to consider a single chromosome count as being sufficient.

Discussion

G. TISCHLER: MRS. MATTICK-EHRENBERGER wrote me a few months ago that she has found a race of *Nasturtium officinale* with $2n=16$. It came from Tyrol near the "Gschnitz-Tal".

I. MANTON (Leeds)

Polyploidy and its Probable Significance in the Pteridophyta

The *Pteridophyta* are characteristically a group with high chromosome numbers, which explains the extreme inaccuracy of almost all previous records. The cytological facts to be quoted are all illustrated photographically in "Problems of Cytology and Evolution in the *Pteridophyta*" MANTON, 1950, a proof copy of which will be on view.

The subject of polyploidy falls into four main topics:

- 1) Occurrence in the various groups within the *Pteridophyta*.
- 2) Causes.
- 3) Consequences.
- 4) Possible sources of further evidence.

Elaborating these:

1. Polyploidy is widespread throughout the *Pteridophyta*, with a few outstanding exceptions, e.g. *Osmundaceae* ($n=22$), *Selaginella* ($n=9$). The highest levels occur in the most ancient groups, e.g. *Equisetaceae* ($n=108$), *Psilotaceae* ($n=ca. 50, 100, 200$), *Ophioglossaceae* ($n=ca. 125, ca. 250$). This cannot be a primitive feature but is likely to be a sign of antiquity. In the polypodiaceous ferns on the other hand there are clear signs in the floras of western Europe that a widespread development of allopolyploid species has occurred fairly recently. The diploid ancestral types are in very many cases still traceable, though their areas are generally disrupted, or in various ways restricted compared with the tetraploids.

2. The cause of the recent epidemic of polyploidy is almost certainly associated with the Ice Age, but the significant factor in this is thought not to be glaciation as such but rather the violent climatic disturbances caused by the succession of glacial and interglacial periods. The zonation of polyploidy with latitude detected in western Europe by LÖVE and LÖVE is thought to express the fact that the most recent major climatic change has been the recession of the last glaciation but similar effects could equally be produced by other types of physical disturbance. This view is supported by the high states of polyploidy found in the ancient groups and in other parts of the world not directly affected by the Ice Age. A detailed comparison between the fern floras of Britain and of Madeira is quoted in illustration.

3. Two very different effects of polyploidy are suggested by the evidence:

a) There seems to be a survival value of polyploids relative to their diploid ancestors both at the time of their formation, by means of which they become established, and also in the course of geological time, which results in the eventual disappearance of most or all the low numbered forms in groups in which polyploidy has been extensively practiced.

b) The accumulation of high chromosome numbers in the ancient groups is perhaps connected causally with a slowing down of their evolutionary potential in species formation. The marked difference between the number of living species in the genera *Equisetum* (24 species, $n=108$) and *Selaginella* (800 species, $n=9$) may be a sign of this. If it is true, one must infer that the evolutionary potential of the Pteridophyta as a whole is running down.

4. Further evidence of two kinds is much to be desired.

(a) The working of other complete small sample floras in different parts of the world for statistical comparison with those of Britain and Madeira. (b) The extension of the cytological study of west European species to

specimens of the same or related species from non-European countries. Any contributions of either fresh spores or live plants that collectors could send would be welcome.

Discussion

R. RUGGLES GATES: This work shows many very high chromosome numbers in Pteridophytes, e.g. $n=108$ in *Equisetum*. Evidence regarding the degree of polyploidy might be obtained by determining the numbers of nucleoli, satellites and secondary constrictions.

P. N. BHADURI: In all the preparations shown, except in those few cases which were polyploidized artificially, there has been no indication of multivalent formations although from the count of the chromosomes it appears that they are very high polyploids. This can only be explained if we assume repeated amphidiploidy during the evolution of these species. It is suggested that critical examination of the chromosomes and nucleoli may indicate whether increase in number of chromosomes could take place by some other method than polyploidy, such as fragmentation of nucleolar chromosomes.

E. K. JANAKI-AMMAL (Ripley, Surr.)

Polyploidy and Migration in the Genus Magnolia

The significance of chromosome numbers in the systematic position of the family Magnoliaceae is presented, and the wandering of *Magnolias* before and after the Ice Age is related to the present distribution of diploid and polyploid species in Asia and North America.

B. LÖVKVIST (Uppsala)

Polyploidy and Differentiation in the Cardamine pratensis Complex

Cytological investigations of plants of *C. pratensis* from a great many localities in western and northern Europe have been made. Be-

cause of a chromosome fusion in tetraploids and higher types resulting in one long chromosome pair instead of two short ones, there have been difficulties in counting the exact number in mitosis. Tetraploids ($2n=30$) have two genomes with seven and two with eight chromosomes. Hexaploids and higher categories have a mixture of genomes with seven and eight chromosomes and thus fluctuations in chromosome number.

Material studied:

Diploids $2n=16$: Portugal, Austria.

Tetraploids $2n=30$: From the Pyrenees to northern Norway.

Hexaploids $2n=42-48$: Central France.

Octoploids $2n=56-64$: Great Britain, Denmark, Finland, Iceland, Norway, Sweden.

Decaploids $2n=72-76$ (-80): Denmark, Iceland, Norway, Sweden.

Ecological differences between the chromosome number groups occur, so that higher chromosome number usually is correlated with higher water content of the soil.

Diploids, tetraploids and decaploids can be separated morphologically, while great difficulties are met with in the hexaploids and octoploids.

Crossings in all directions within the complex have been made. Very few sterility barriers seem to be absolute excepting those between diploids and most other types. Hybrids between tetraploids and other races are difficult to obtain. Successful crossings within the octoploids and between octoploids and decaploids are easily made. Very often artificial pollination between plants of different chromosome numbers gives a better seed setting than pollination between plants of the same race: crossings within the race $2n=60$ have an average seed setting of 12.19 seeds per silique, but pollinated with pollen from plants with $2n=64$ the seed setting was 15.74.—Crossings between tetraploids ($2n=30$) and plants in the octoploid group ($2n=56-64$) give a hexaploid progeny which is highly fertile. These hybrids are also fully fertile

with spontaneous hexaploids from France.—Hybrids between tetraploids and decaploids ($2n=72-76$) and between octoploids and decaploids have a decrease in pollen quality but the seed setting is nearly the same as in the parents.

Successful interspecific crossings have been made between diploid *C. pratensis* and *C. amara* ($2n=16$). Hybrids between *C. flexuosa* ($2n=32$) and tetraploid *C. pratensis* are very easy to obtain but up to now only with *C. flexuosa* as the female. All plants from this species cross are highly sterile.

Discussion

M. GUINCHET: M. LÖVKVIST dit qu'il ne connaît la forme à $2n=16$ de *Cardamine pratensis* que du Portugal. Or j'ai signalé l'existence de cette forme dans le Jura français dès 1946 (*c.r. Acad. Sc. T.* 222) où elle existe avec des formes à $2n=30$ et à $2n=40$; mais ces formes à nombres de chromosomes différents vivent dans des associations végétales distinctes; c'est d'ailleurs ce fait qui m'a amené à étudier la caryologie de *Cardamine pratensis*; la phytosociologie constitue du reste une excellente méthode pour la mise en évidence méthodique des écotypes ainsi que je me propose de le développer dans une communication initialement destinée à être lue devant la section de Taxonomie expérimentale, mais qui a été inscrite à celle de Phytogéographie, pour une raison que j'ignore.

R. NORDHAGEN: May I ask whether Dr. LÖVKVIST has studied the race of *Cardamine pratensis* in the high mountains of Sweden and Norway. This race has been called *dentata*, it very often propagates vegetatively from the leaves and thrives in rivulets or cold springs, often in "Schneetälchen." It looks indeed very different from the low-land races.

B. LÖVKVIST: I have made some studies and have found that the mountain races are different from the low-land ones. In my opinion none of these races are *Cardamine dentata* Schultes.

D. H. VALENTINE: Do you happen to know anything about the pollination mechanism of *C. pratensis*, do you know if the species is self-compatible? These points are of interest in arguing how different forms of the species growing in contiguous habitats are isolated from one another.

B. LÖVKVIST: As far as I know, self-incompatibility is normal in most races, and the development of the sex apparatus indicates true allogamy contrary to the conditions in many other species of the genus: *C. hirsuta*, *C. impatiens*, *C. flexuosa* and *C. amara*.

G. A. L. MEHLQUIST (St. Louis, Mo.)

Polyploidy in Orchid Genera of Commercial Importance

In recent years three phenomena have been apparent to orchid breeders, namely:

1. Some stud plants have a much greater influence on the progeny than others of the same apparent qualities.
2. Increased sterility often results from the use of such exceptional stud plants.
3. These exceptional stud plants are usually of heavier texture than others and usually transmit this feature to the progeny.

As these characteristics often are the result of polyploidy a cytological investigation was undertaken to ascertain whether this was the case. So far these studies have been directed primarily at three genera namely *Cattleya*, *Cymbidium*, and *Paphiopedilum* (*Cypripedium*). In addition, the chromosome numbers have been determined for *Brassavola digbyana* and *Laelia purpurata* as these two species together with *Cattleya* form the basis for most of the *Brasso-Cattleya*, *Laelio-Cattleya* and *Brasso-Laelio-Cattleya* hybrids of horticultural importance. The results that have been obtained to date may be summarized as follows:

Brassavola digbyana $2n=40$.

Cattleya Bowringiana, *C. Dowiana*, *C. Dow. var. aurea*, *C. Gaskelliana*, *C. Harrisoniana*, *C. labiata*, *C. Loddegesii*, *C. Mossiae*, *C. Percivaliana*, *C. Schroederi*, *C. Trianaei*, *C. War-*

neri, *C. Warscewiczii*, $2n=40$. One tetraploid form (var. *splendens* Hort.) was found in *C. Bowringiana* and one triploid and one tetraploid form was found in *C. Trianaei*.

Laelia purpurata $2n=40$.

Brasso-Cattleya, *Laelio-Cattleya*, and *Brasso-Laelio-Cattleya* are usually diploid with $2n=40$ but many commercial progenies are triploid and occasionally tetraploid indicating the use of tetraploid stud plants.

Cymbidium. The ten species that are common in horticulture and are the parents of the present day hybrids, *C. eburneum*, *C. erythrostylum*, *C. grandiflorum* (Hookeri), *C. P'Ansoni*, *C. insigne*, *C. Lowianum*, *C. Parishii*, *C. Par. var. Sanderæ*, *C. Schroederi*, *C. Tracynum* are diploid with $2n=40$. Two well-known hybrids that have been widely used as stud plants, *C. Alexanderi*, WESTONBIET variety and *C. Pauwelsii* var. COMPTE DE HEMPTINNE are tetraploid with $2n=80$ and have been used in raising large progenies of triploids and some tetraploids.

Paphiopedilum (*Cypripedium*). The haploid number varies from 13 to 20. Triploids, tetraploids and aneuploids as well as diploids are common in horticulture. (Mo. Bot. Gard. Bull. 35 (10); 211-228. 1947.)

The evidence indicates that orchid growers in selecting forms of greater size and heavier texture as being more desirable for horticultural purposes are increasing the polyploidy in genera of commercial importance. Orchid breeding in the future will undoubtedly be directed toward the production of triploids as such polyploids seem to possess sufficient increase in size and texture without undue loss of productivity.

N. W. SIMMONDS (Trinidad)

Polyploidy in Bananas

Wild Musas are all diploid, with 20 or 22 chromosomes. Cultivated bananas are derived from two species in the 22-chromosome group and are diploid ($2n=22$) or triploid ($2n=33$).

Higher polyploids have been produced experimentally.

Origins of polyploidy. Study of certain diploid interspecific hybrids has shown that diploid and tetraploid spores may be produced by an unusual mode of restitution in which the second or both divisions of meiosis fail and are replaced by a sort of endomitosis. Such spores are functional on the female but not on the male side. The same mode of formation of polyploid spores has been observed rarely in material other than interspecific hybrids (e.g. certain edible varieties) and is believed to be the main or even sole source of natural polyploidy in bananas.

Characters of polyploids. Surveys of collections of mature bananas ranging from diploid to pentaploid showed that:

(1) Stomatal size increases approximately linearly with ploidy.

(2) Maximal vigour is attained at triploidy-tetraploidy, pentaploids being weakly and higher polyploids virtually inviable.

(3) The higher the ploidy (up to pentaploidy, at least) the thicker and more flaccid are the leaves which have a characteristic drooping habit correlated with a low percentage dry weight of the petiole.

(4) The veneration of a banana leaf is convolute and constant; in diploids neither half of the lamina is apparently restricted in development and the right half is generally broader than the left. The reverse is true of polyploids and the narrow right half of the leaf (that internal in veneration) is variably wrinkled and distorted near the margin, a sign of restriction of space for development. The inequality and distortion increase with increasing ploidy.

Differences in vigour and leaf characters between triploids and pentaploids could not be detected in very young seedlings but were clearly apparent later. With regard to leaf thickness, those parts of the lamina which were latest to differentiate were more affected by ploidy than parts which had a shorter developmental history. It is concluded that

ploidy has an immediate, generalized effect on cell-size (and, probably, on rate of cell division) and, also, a number of secondary effects which are expressed developmentally. The later the stage in the development of the plant or one of its organs, the greater are the effects of ploidy.

Significance. Most cultivated banana varieties are triploid and have probably been selected by man for their superiority over diploids in vigour. No naturally-occurring tetraploids are known though mechanisms for their production are; this is a curious fact since it is known that they are only slightly or not at all inferior to the triploids in vigour. Indeed, the banana breeding programme against Panama Disease rests on the production of primary tetraploids by crossing the edible triploid Gros Michel ($2n=33$) by various diploids ($2n=22$), Gros Michel contributing unreduced female gametes with 33 chromosomes.

A. F. BLAKESLEE (Northampton, Mass.)

*Demonstrations of a Horticultural Type
Developed from a Wild Weed,
Rudbeckia hirta*

Colored photographs were shown of flowers of types of the Black-eyed Susan (*Rudbeckia hirta*) which have been developed during the past 40 years from a relatively small-flowered wild type. In nature the species is highly variable in respect to many floral characters. By crossing large-flowered types from different localities an accumulation of genes for large size has been secured. Similarly the number of rays has been increased and double flowered types secured by combining genes for large number of rays from different places. Doubling chromosome number by colchicine treatment has resulted in strains with still larger flowers and deeper ray color. Many of the flowers are well over 6 inches in diameter and a few have reached 10 inches. In addition to double-flowered strains, single-flowered

types have been developed with a mahogany blotch at base of each ray. The Black-eyed Susans furnish an example of what can be accomplished in developing an attractive horticultural type from a neglected weed.

G. TISCHLER (Kiel)

Die Basiszahlen der Chromosomen innerhalb der natürlichen Ordnungen und Familien bei den Angiospermen

Gegenüber der grossen Einförmigkeit, die anscheinend für die Basiszahlen der meisten *Lycopodiaceen*, *Isoetaceen*, *Equisetaceen*, *Coniferen* und *Gnetaceen* gilt, muss die oft ausserordentlich grosse Variabilität der Basiszahlen bei den Angiospermen auffallen. Der Sonderfall, dass alle Daten sich auf eine Zahl zurückführen lassen, ist nur selten verwirklicht. Welche Zahl bei Annahme monophyletischer Entstehung einer Familie die „eigentliche“ Basiszahl ist, lässt sich meist nicht feststellen. Organographische und pflanzengeographische Studien könnten vielleicht zur Aufklärung beitragen. Seit BABCOCKS Untersuchungen an *Crepis* wissen wir, dass durchaus nicht die niedrigste Zahl die Basiszahl zu sein braucht.

Bei einem ersten Typ haben wenigstens die einzelnen Unterfamilien eine annähernd konstante Zahl. Hierher gehören die *Rosaceen* und *Gramineen*. Relativ wenige Ausnahmen kommen hier vor.

Ein zweiter Typ zeigt oft parallel laufenden Wechsel in den benachbarten Unterfamilien, daneben aber kleinere mit konstanter Zahl. Beispiele bieten die *Leguminosen*, *Crassulaceen-Saxifragaceen*, *Papaveraceen*.

Trotzdem können die bekannten Zahlen phylogenetisch benutzt werden, so bei *Solanaceen*, *Ranunculaceen*-*Berberidaceen* und *Cruci-*

feren. Geht man bei letzteren von JANCHENS System aus, ergibt sich, dass die als ursprünglich angesehenen Unterfamilien $b=7$ besitzen. In den abgeleiteten tritt oft $b=8$ auf, manchmal allein. Nur in der anscheinend jüngsten, den *Brassicaceen*, ist die Variabilität stark gestiegen. Darunter befinden sich, durch das Experiment verifiziert, Amphidiploide. Für die aussereuropäischen abweichenden Unterfamilien, die starke Beziehungen zu den *Capridaceen* aufweisen, fehlen Untersuchungen.

Mit grosser Typenmannigfaltigkeit ist meist grosse Variabilität der Basiszahl verbunden (*Compositen*, *Leguminosen*, *Liliaceen*, *Labiataen*, *Scrophulariaceen*, *Caryophyllaceen*). „Reduktionsreihen“ zeigen oft Abnahme der Variabilität, so innerhalb der Centrospermen die *Plumbaginaceen*, *Aizoaceen*, *Portulacaceen* und *Chenopodiaceen*. Auch die *Cactaceen* schliessen sich an. Nur eine Basiszahl, dazu sicherlich eine „sekundäre“, zeigen solch abgeleitete Familien wie die *Fagaceen*, *Salicaceen*, *Typhaceen*, *Sparganiaceen*, *Potamogetonaceen*. Das entgegengesetzte Extrem repräsentieren die *Cyperaceen*, bei denen überhaupt keine Basiszahl zu erkennen ist. Die Dysploidie macht es hier unmöglich.

Bisweilen lässt sich die Übereinstimmung der Basiszahlen als Argument für engere phylogenetische Beziehungen verwerten. Das zeigt die Reihe der *Araliaceen*, *Hydrocotylaceen*, *Umbelliferen*, *Cornaceen*, *Garryaceen*, *Rubiaceen*, *Caprifoliaceen*, *Adoxaceen*.

Alle Schlüsse sind nur vorläufige, da von den ca. 160 000 bekanntgewordenen Angiospermen erst ca. 10 % chromosomal untersucht sind. Die meisten Arten stammen aus den kalten und gemässigten Zonen. Die Species der Tropen und Subtropen dürften uns noch viele Überraschungen zeigen.

SESSION 4

July 17th, 9 a.m. — noon

Chairman: D. G. CATCHESIDE

SUBJECT:

Various Papers

K. MATHER (Birmingham)

The Genetical Architecture of Heterostyly in Primula sinensis

Pin and thrum plants of *P. sinensis* differ in five characters, length of style, position of anthers, size of stigmatic pappillae, size of pollen grains, and incompatibility properties of pollen and style. The five characters are switched as a single unit by a single gene (*Ss*=Thrum; *ss*=Pin). *SS* plants produced in experiment are thrums indistinguishable from the usual *Ss* type. No other allelomorphs of this gene are known in this species, as have been found by ERNST and others elsewhere in the genus.

Two genes of major action are known to affect the expression of heterostyly. The recessive "fertile double" (*mm*) raises the anthers without affecting the style and the recessive "Primrose Queen" (*aa*) shortens the style, without affecting the anthers. Thus in the pin series *ssMMaa* is a short homostyle and *ssmmAA* is nearly a long homostyle. The combination, *ssmmaa* gives a pseudo-thrum plant, while *Ssmmaa* gives an extreme or super-thrum.

The expression of at least one of the characters, style length, is also affected by modifying genes which constitute a polygenic system. Thus some genetically normal pins have longer styles than others. There is evidence of weakening in the incompatibility character by the selection of a polygenic system during the horticultural exploitation of *P. sinensis*. Inbred pin plants show more variation in style length between flowers of the same plant than

do cross-bred plants, i.e. development variation is greater in inbred than in crossbred plants. Development is most regular in the type of plant normally produced by the mechanism of heterostyly.

The actions of *m* and *a* show that at least some of the five characters, normally switched as a unit by the *S-s* difference, are separable in development and heredity. Their apparent unity is synthetic. It has been built up by selective adjustment of the major genotypes (comprising such genes as *M-m* and *A-a*) and of the polygenotype.

It would seem equally true that the switch-gene itself (*S-s*) must have been built up piecemeal to control all five characters simultaneously, for it could hardly be an accident that it simultaneously and uniformly switches five characters which are themselves separable. The variety of allelomorphs discovered by ERNST to give various combinations of the characters confirms this gene's composite nature. The controlling subgenes, if ERNST's units may be so designated, have presumably come to be together by their evolution in adjacent positions which may have involved the development of new juxtapositions by structural change. The occurrence of a small inversion associated with *S-s* would serve to bind the sub-genes indissolubly together into a super-gene as they seem to be in *P. sinensis*. This has presumably not occurred in species where the sub-genes are capable of re-association.

The evolution of heterostyly must have involved the constructive evolution of the allelomorphs of the switch gene, as well as of the

main (and normally invariable) genotype governing the coordinated development of the pin and thrum forms.

Discussion

H. G. BRUN: Do *A* and *M* belong to the same linkage group?

K. MATHER: No, they are independent.

H. G. BRUN: When discussing the question of the origin of heterostyly in *Primula* in general, we must remember that there are primary and secondary cases of heterostyly as well as primary and secondary homostyly. The latter has certainly originated in different ways in different sections. In the section *Farinosae* homostyly is correlated with polyploidy. All heterostyled species are diploid and all homostyled are polyploid.

J. L. CROSBY (Durham)

The Selection of Unfavourable Genes

Many, if not all, genes are pleiomorphic. In organisms with alternation of dissimilar generations it should be possible for an allele to have quite different effects in the two generations and be subject to selections differing in magnitude and in sign.

Further, the nature of competition may be different in the two generations. Sporophytic competition is both intraspecific and interspecific, but gametophytic competition may be almost entirely intraspecific with no immediate effect on species numbers. In flowering plants for example, competition between pollen grains is entirely for ovules, and is intraspecific except where two pollen-compatible species are growing together; change in gene frequency here will have no immediate effect on species numbers unless there is a change in the proportion of ovules fertilized.

An allele giving an advantage to pollen grains will be selected during the gametophyte generation. But the same allele may have a harmful effect on the sporophyte and thus be selected against in that generation, with ac-

companying decrease in species numbers. The fate of this allele will depend on the balance between the two selections. If its selection during the gametophyte generation is greater than selection against it during the sporophyte generation, the allele will increase in frequency and species numbers will fall.

Such a situation can be imagined in a simple form, but there is no evidence yet to suggest that it does so exist. But already published evidence from *Primula* suggests that the sudden transformation of a specialised outbreeding mechanism to partial inbreeding may provide the conditions for such a phenomenon, if the allele responsible for the change was once normally heterozygous and now becomes homozygous, the homozygote being harmful. The upset of specialised breeding systems seems to be the most likely place to look for the selection of unfavourable genes, but simpler possibilities should not be neglected. There seems to be no reason why such a phenomenon should be very rare, but if it proves to be so this may suggest that there is some unsuspected evolutionary mechanism checking it.

Such an accident of evolution could cause a serious decline or even rapid extinction of a species, unless selection of modifiers or alleles reducing the sporophytic disadvantage supervenes. How common or important this has been, further work may show, but at least it is of some philosophic interest, and may perhaps help to solve a few of the smaller problems of evolution.

Discussion

J. W. LESLEY: A successful homostyled self-fertile species may perhaps arise from a heterostyled species by the mechanism suggested in Crosby's paper.

H. G. BAKER: There appears to be considerable similarity between the origin of homostyly in *Primula vulgaris* and that of monomorphism in *Armeria maritima* and in *Limonium*. In the first case, at least, there is a likely adaptive effect of inbreeding, for where the species occurs

in Arctic regions, a monomorphic form which shows no inbreeding depression is found.

K. MATHER: Genes having two effects, one favourable and the other unfavourable may lead to equilibrium. It is, however, possible that they would cause the extinction of the population. HUXLEY has suggested that some animal species may have become extinct for this reason.

F. CHODAT (Genève)

*Gènes de tempérament et développement phasique chez *Daucus carota**

Nous avons établi une classification des cultigènes de *Daucus carota*, fondée sur les caractères de la forme des racines: corps conique ou cylindrique, épaules tombantes ou droites, base pointue ou obtuse. La nature héréditaire et le comportement mendélien de ces caractères sont prouvés par les faits suivants: 1) ces caractères définissent des variétés, entités génétiques connues des praticiens et des hybrideurs pour la fixité de leur forme; 2) des croisements opérés par F. FRIMMEL, puis par nous, confirment par les manifestations de dominance (conique domine cylindrique) et de ségrégation la nature allélique de ces caractères.

L'étude attentive des variétés Nantaise et Nantaise-Touchon révèle des faits qui rendent difficile en première approximation, l'adoption de l'hypothèse factorielle sus-énoncée. Voici le principe qu'impliquent ces faits: l'importance relative des classes de phénotypes, manifestée par les portions similaires d'un même lot de graines, varie en fonction des conditions climatiques.

Deux techniques nous ont permis d'observer et de mesurer ce phénomène. Technique 1: semer en 1947, 1948 et 1949 les graines d'un lot commun et estimer au moment de la récolte l'importance relative des classes de phénotypes (semences fournies par F_1 issus d'autofécondations opérées sur des sujets d'élite d'un lot sélectionné). Technique 2: opérer au cours d'une même année (1949) des semis successifs et procéder aux mêmes estimations

pour chacune des récoltes obtenues; semis aux 1 avril, 1 mai, 1 juin, 15 juin, 1 juillet et premier août; récolte après 4 mois. Voici l'un des résultats fournis par cette seconde technique: sur 100 racines potentiellement cylindriques, le semis d'avril donne 44 cylindriques, celui de mai 100, celui de juin 95, celui du 15 juin 50, celui de juillet 16 et celui d'août 6. Certaines conditions climatiques (le froid) entravent l'expression du caractère cylindrique chez un cultigène de carotte. Il faut donc abandonner l'idée qu'une population de ce légume exprimera intégralement toutes ses potentialités d'année en année.

La nature incontestablement mendélienne du caractère cylindrique et les observations de phénogénétique rapportées plus haut, deviennent compatibles dans le cadre de la génétique classique à condition d'envisager l'existence de gènes de tempérament. Certains caractères, apparemment instables et fréquents chez les cultigènes, doivent leur réalisation à l'effet conjugué de deux facteurs au moins. L'un d'entr'eux préside au tempérament de la variété, soit un caractère héréditaire de sensibilité à la température ou au photopériodisme. Si le sujet n'a pas bénéficié au moment voulu de l'influence thermique ou lumineuse appropriée, il n'exprimera pas le caractère attendu. L'inégalité climatique d'années ou de cycles culturaux différents, est à l'origine de ces bénéfices manqués.

Ces recherches ont été faites avec la collaboration de M. FRANÇOIS GAGNEBIN à la Station de Botanique Expérimentale de l'Université de Genève.

F. GALÁN (Salamanca)

*Analyse génétique de la monoecie et de la dioecie zygotiques et de leur différence dans *Ecballium Elaterium**

J'ai constaté que les populations de *E. E.* sont monoïques dans plusieurs localités de la moitié N. de l'Espagne et dioïques dans plusieurs localités de la moitié S.

J'ai identifié ces variétés avec celles que

BATTANDIER découvrit en Algérie et décrit comme *E. E. monoicum* et *E. E. dioicum*.

J'ai effectué quelques croisements à partir de ces variétés avec les résultats suivantes:

$F_1 (\varnothing m \times \varnothing m)$	22 ♀	
$F_1 (\delta d \times \varnothing d)$	135 ♂	132 ♀
$F_1 (\varnothing m \times \varnothing d)$	881 ♀	
$F_1 (\delta d \times \varnothing m)$	423 ♂	4 ♀
$F_2 [(\varnothing m \times \varnothing d) \text{ vel } (\delta d \times \varnothing m)]$	2 ♂	16 ♀
$F_2 (\delta d \times \varnothing m)$	105 ♂	7 ♀
$F_1 [\delta d \times \varnothing F_1 (\delta d \times \varnothing m)]$	48 ♂	35 ♀
$F_1 [\varnothing F_1 (\delta d \times \varnothing m) \times \varnothing m]$	483 ♂	3 ♀
$F_1 [\varnothing F_1 (\delta d \times \varnothing m) \times \varnothing m]$	58 ♀	1 ♀

Tous ces résultats peuvent être expliqués si l'on suppose que:

1° a^+ , a^D , et a^d forment une série d'allèles multiples;

2° a^D produit ♂ et domine sur a^+ , a^+ produit ♀ et domine sur a^d , et a^d produit ♀;

3° le phénotype correspondant aux génotypes qui possèdent a^+ et ne possèdent pas a^D , est un peu modifiable, de manière qu'il peut être avec la même proportion (toujours inférieure à 10 pour 100) ♂ comme ♀;

4° *E. E. monoicum* comporte a^+ , et *E. E. dioicum* comporte a^D et a^d .

Discussion

A. HEILBRONN: *Bryonia dioica* und die süd-anatolische *Bryonia multiflora* sind beide diöcisch, lassen sich kreuzen und liefern ausschliesslich ♀ Bastarde. Diese ♀ Bryonien sind nicht identisch mit *B. alba*, sie werden als die gemeinsame Stammform von *B. dioica* und *multiflora* betrachtet, aus der sie durch 2 verschiedene nicht alle Mutationsschritte hervorgegangen sind. Die Zwitterigkeit bei dieser Stammform muss also mindestens bifaktoriell bedingt sein.

P. MICHAELIS (Voldagen/Elze)

Ergebnisse der Plasmavererbung und ihre Bedeutung für das Artbildungsproblem

Die geringe Bewertung des plasmatischen Erbgutes für die Evolution ist aus folgenden Gründen einer Revision zu unterziehen:

(1) Aus der Häufigkeit reziprok verschiedener Bastarde darf nicht auf die Verbreitung plasmatischer Erbunterschiede geschlossen werden. Reziprok verschiedene Bastarde können nur dort erwartet werden, wo das Plasma von der Mutter geliefert wird und geeignete Genotypen die Manifestation plasmatischer Unterschiede gestatten (1).

(2) Es kann in einem bestimmten Plasma die Mutationsrate der Kerngene verändert (2) und einzelne Gene labil werden (3).

(3) Es können durch das Erbplasma die Manifestationsmöglichkeiten und der Wirkungseffekt der Kerngene wesentlich verändert werden. Es lässt sich z. B. in der (*Epilobium hirsutum* Jena × München) × *E. luteum*-Kreuzung eine polygene, in den reziproken Kreuzungen dagegen eine im wesentlichen nur monogene Spaltung feststellen (4). Es wurden bei *Epilobium parviflorum* röntgeninduzierte Genmutanten gefunden, die bei *E. parviflorum* rezessiv, sich doch im Plasma des *E. hirsutum* Essen × *parviflorum*-Bastard manifestierten. 1 Mutante manifestierte sich sogar nur im Plasma dieses Bastardes, nicht in der Entstehungssippe (5). Die durch Einlagerung von Genen aus dem atlantischen Verbreitungsgebiet der Art *E. hirsutum* in ein in Mitteldeutschland weiter verbreitetes Plasma entstehenden polsterförmigen Wuchsformen (6) sind besonders gut an niedere Temperaturen angepasst und hier den hochwüchsigen Wuchsformen im eigenen Plasma überlegen.

(4) Das Erbplasma oder Plasmon ist eine Summe verschiedener Erbkomponenten (7), die durch Mischung väterlichen und mütterlichen Plasmas bei der Befruchtung abänderbar ist. Man kann den Sinn der Oogamie darin sehen, dass die Erhaltung plasmatischer Erbunterschiede erleichtert wird (7). Wesentlich ist, dass diese plasmatische Erbsumme während der ontogenetischen Entwicklung eines Individuums abgeändert werden kann (8). Die auf solche Weise entstehenden Plasmotypen besitzen einen verschiedenen Selektionswert, der schon innerhalb des Individuums effektiv werden kann. Auf diese Weise können,

allerdings nur unter bestimmten Bedingungen, eine fließende Variabilität (9) und Übergänge zwischen erblicher Abänderung, Dauermodifikation, Nachwirkung und Modifikation (10) entstehen, die alle mehr oder minder auf eine Beseitigung von Entwicklungsstörungen ausgerichtet sind (11). Eine „Vererbung erworbener Eigenschaften“ wurde bisher nicht beobachtet. Es kann die Hypothese aufgestellt werden, dass manche entwicklungsphysiologischen Vorgänge, die im Laufe der Ontogenie zu einer Differenzierung und Determinierung führen, auf solche reversiblen oder irreversiblen Abänderungen des plasmatischen Erbgutes zurückzuführen sind (8, 12).

(5) Da in den Untersuchungen die reziproken Unterschiede (Letalität, Sterilität, Geschlechtsverschiebung, Heterosis, Wuchsunterschiede und mannigfache, wichtige Merkmale der Form und Farbe) weder von den Kerngenen noch vom Plasma allein abhängig sind (13, 14), lässt sich die Hypothese aufstellen (12, 15), dass der Phänotyp durch ein Erbsystem aus genetischen und plasmatischen Erbtägern bestimmt wird, in dem nicht nur die Eigenart der Systemglieder, sondern auch die Ordnung des Systemganzen für die Gestaltung des Phänotyps massgeblich sind. Es hängt in diesem Falle von der Versuchsmethodik ab und von dem Zeitpunkt, zu dem die untersuchten Systemglieder in die Reaktionsabläufe eingreifen, ob in einem Versuch die Wirkung des Erbplasmas oder der Kerngene oder des Systemganzen erfasst wird.

Auf der Basis eines solchen genetischen Systemes sind für die Erklärung der Evolution neue Möglichkeiten gegeben: Beispielsweise scheint eine Evolution nur durch die harmonische Veränderung des Gesamtsystemes möglich zu sein. Die stärkere Abänderung eines einzelnen Systemgliedes z. B. durch Genmutation wird stets zu Systemstörungen, zu Letalität und Sterilität führen. Solche durch Mutation entstehenden Entwicklungsstörungen sind vor allem systembedingt und durch Abänderung des Gesamtsystemes zu beseitigen. Die relativ leichte Abänderbarkeit des Plas-

mas bietet hierzu neue Wege. So wurde im Experiment eine Beseitigung genbedingter Entwicklungsstörungen durch Plasmonabänderung im Laufe der Ontogenie beobachtet (16). Ganz allgemein wird die Bedeutung der Genmutation wesentlich von der Struktur des Gesamtsystemes bestimmt werden. In einem wenig koordinierten System werden einzelne Mutanten sich nur schwach manifestieren und die Mutantenhäufigkeit relativ gering sein. In einem stark spezialisierten System werden Mutationen zu starken Abweichungen führen. Es werden bei stärkster Spezialisierung die Mehrzahl der Mutanten letal sein. Typogenese, Typostase und Typolyse könnten vielleicht hierdurch zu kennzeichnen sein. Weiterhin kann in einem genetischen System die Änderung des Systemganzen zeitlich weitgehend unabhängig von der Änderung der Systemglieder erfolgen. Eine explosive Formentwicklung muss nicht mit einer entsprechenden Zunahme der Mutationshäufigkeit verknüpft sein.

Wenn an der Merkmalsausprägung nicht nur die Qualität der einzelnen Erbtäger, sondern auch die Struktur des genetischen Systemes beteiligt ist, so ist es verständlich, dass ausgesprochene Bauplanmutanten bisher nicht gefunden wurden. Es wäre auch zu erwarten, dass durch eine gegebene Systemordnung die Entwicklungsmöglichkeiten begrenzt werden und dass damit eine orthogenetische Entwicklung vorgetäuscht wird. Da nach den bisherigen Erfahrungen Abänderungen des plasmatischen Erbgutes bevorzugt im Laufe der ontogenetischen Entwicklung vor sich gehen und vermutlich an den ontogenetischen Differenzierungen beteiligt sind, so wäre auch das „ontogenetische Grundgesetz“ von HAECKEL einem kausalen Verständnis zugänglich.

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Discussion

H. FITTING: Die Ausführungen des Herrn MICHAELIS, dass sektorale Entmischungen auf Plasmonmutationen beruhen sollen, scheinen doch den Gedanken nahezulegen, dass daran Plastidenentmischungen beteiligt sind. Ferner, wie lässt es sich verstehen, dass bei *Epilobium* in der Ontogenie Plasmonmutationen häufig sind, während FR. VON WETTSTEIN etwas derartiges bei seinen Moosen nicht beobachtet hat?

H. ROSS (Voldagsen/Elze)

Physiologie der Reziprokenunterschiede bei einigen *Epilobium*-Bastarden

Kreuzungen einer Sippengruppe A ♀ mit einer Sippengruppe B ♂ von *Epilobium hirsutum* ergeben F₁-Bastarde mit Wuchsstörungen, deren Ausmass von der verwendeten Vatersippe abhängt. Die reziproken Bastarde sind normal. — Zur physiologischen Untersuchung kamen Bastarde der Sippe Jena (Gruppe A) ♀ mit 22 Sippen der Gruppe B ♂. Sie bilden eine Skala mit abgestuften Hemmungsgraden von unmerklichen bis fast letalen Wuchsstörungen (Hemmungsreihe). Es wurden folgende physiologische Unterschiede gegenüber den normalen Gegenkreuzungen festgestellt: Unterbindung der Anthozyanbildung nach Massgabe der verwendeten Vatersippe, Hemmung der nächtlichen Stärkeableitung, Steigerung der Aktivität der Katalase, der Peroxydase und der Atmung, sowie Abschwächung der Kurztagmerkmale. Durch Zufuhr von Heteroauxin wurden in gewissen Wachstadien

die Wuchshöhenunterschiede aufgehoben. Durch Kultur bei 10–15° werden die Störungen weitgehend kompensiert. Da die Unterschiede in der Peroxydaseaktivität besonders eindeutig waren, wurden diese im Verlauf der Gesamtentwicklung der Pflanzen im Reibsaft des Sprossgipfels in dreijähriger Wiederholung verfolgt. Die Peroxydaseaktivität nimmt während der Phasenfolgen einen kurvenförmigen Verlauf mit einem Maximum in der Kurztagphasen und einem Minimum während der Langtagphasen. Die Werte der südlichen Sippen liegen hierbei etwas unter denen der nördlichen Sippen, in welch letzteren sich die Sippe Jena ohne Besonderheiten einfügt. Die Werte der gestörten Bastarde Jena ♀ × Sippengruppe B ♂ liegen während des ganzen Kurvenverlaufs weit über den Werten der normalen Gegenkreuzungen und der Elternsippen, und zwar umso mehr, je grösser die Störung des Bastards ist. Die Wuchsunterschiede der reziproken Bastarde wechseln im Verlauf der Entwicklung: im Stadium des Übergangs von der Rosette zum Laub- und Blühspross ist das Wachstum der Bastarde mit Jenaplasmon sogar gefördert gegenüber denen der normalen Gegenkreuzungen. Trotzdem sind die Unterschiede in der Peroxydaseaktivität stets gleich gross. Sie liegen bei den mittelstark gehemmten Bastarden 20–70 % und bei den stark gehemmten Bastarden 100 % und mehr über den Werten der normalen Gegenkreuzungen. Aus dieser Unabhängigkeit der Peroxydaseaktivitätsdifferenz der Reziproken von modifikativen Einflüssen wird geschlossen, dass in der Steigerung der Peroxydaseaktivität ein physiologischer Prozess gefunden ist, welcher nur relativ wenig Reaktionen weit von den plasmonischen Induktoren entfernt liegt. Andererseits weisen die übrigen physiologischen Unterschiede darauf hin, dass die Peroxydaseaktivitätssteigerung nur der Ausdruck einer Steigerung des gesamten oxydativen Niveaus, vielleicht des Redoxpotentials der Bastarde ist.

Die genetische Analyse der Hemmungen durch MICHAELIS hat die Beteiligung zahl-

reicher Gene erwiesen. In Verbindung mit der physiologischen Analyse folgt daraus, dass normalerweise ein beliebiges Sippenplasma der Gruppe B mit zahlreichen Genen und deren verschiedensten Allelen stets das gleiche Produkt in Gestalt einer normalen Peroxydaseaktivität liefert. Das Jenaplasmon aber bildet nur mit einigen Allelen eine normale Peroxydaseaktivität, mit anderen sehr abweichenden Allelen dagegen eine abnorm erhöhte Peroxydaseaktivität. Das Jenaplasmon ist schwächer „gepuffert“ oder es besitzt eine engere „Karenz“ als die Plasmone der Sippengruppe B. Da die Plasmonvarianten von MICHAELIS auf die Zusammensetzung des Plasmons aus einer Anzahl von Komponenten hinweisen, können die Plasmonunterschiede möglicherweise in unterschiedlichen Zahlenverhältnissen ihrer Komponenten begründet sein.

R. LINDER (Strasbourg)

L'incompatibilité dans Oenothera missouriensis

L'autostérilité dans *Oenothera Missouriensis*, signalée par Gates, a été retrouvée sur une population du jardin Botanique de Strasbourg. Certaines jeunes plantes de première année présentent un faible degré d'autofertilité qui disparaît au cours des années suivantes. Ni la pollinisation en bouton, ni la pollinisation répétée n'induisent l'autofertilité. Il y a autostérilité, interfertilité, mais aussi interstérilité.

Les ségrégations observées dans la descendance des croisements (4 groupes ou 2 groupes de compatibilité dans une famille) révèlent une incompatibilité du type *Nicotiana* ou *Veronica*, conditionnée par une série multiple S d'allèles d'opposition.

La réaction d'inhibition se fait dans la partie supérieure du style (0 à 4 cm sous les stigmates) sans qu'il y ait de zone d'inhibition déterminée.

Discussion

C. HARTE: Die Bilder zeigen, dass zwischen einer Hemmung der Pollenkeimung durch an-

geschnittene Gewebestücke der Griffel und der Hemmung des Pollenschlauchwachstums durch die Hemmstoffe des unverletzten Griffels unterschieden werden muss.

H. MARQUARDT: Der in vitro Keimungsversuch zeigt, dass neben wachstumshemmenden Stoffen auch noch andere Stoffe eine Rolle spielen (Nekro hormone), die das gezeigte Ergebnis verursachen.

J. POLITIS (Athens)

Sur des gènes produisant de l'anthocyane chez quelques Convolvulées

En 1911, nous avons montré par l'étude de la formation cytologique des pigments anthocyaniques des pétales de fleurs, appartenant aux familles les plus différentes (*Iris fimbriata*, *Laelia anceps*, *Aquilegia glandulosa*, *Erica carnea*, *Nepeta glechoma*, *Clerodendrom Baljoui*, *Weigela rosea*, *W. Japonia*) que ces pigments apparaissent d'abord dans le cytoplasme au sein de corpuscules spéciaux que nous avons désignés sous le nom de cyanoplastes. Ces corpuscules sont très réfringents sphériques et possèdent une enveloppe, dans l'intérieur de laquelle se trouve un composé phénolique incolore qui se transforme en anthocyane. Ensuite, GUILLERMOND (1914) a constaté la présence des cyanoplastes dans les fleurs d'*Iris Germanica*. Des cyanoplastes ont été aussi rencontrés, par nous, dans les plantules de *Raphanus sativus* et d'autres Crucifères et dans les anthères des fleurs de *Pyrus communis* et d'autres plantes.

Dans cette note nous resumons les observations, que nous avons fait sur la formation cytologique de l'anthocyane dans les plantules et les anthères des fleurs de certaines Convolvulées.

Ipomaea purpurea. En examinant de jeunes plantes, quelques jours après le commencement de la germination, nous voyons que l'hypocotyle présente une coloration violette due à la présence d'anthocyane, qui est localisée dans les cellules de l'assise située au-dessous de l'épiderme. Chacune de ces cellules,

à son âge jeune, renferme outre le noyau et les chloroplastes, certains corpuscules à côté du noyau, réunis en un assemblage en forme de grappe. Ces corpuscules, très petits et incolores, tout d'abord, s'accroissent peu à peu, prennent une coloration violette et finalement ils disparaissent. Au cours du développement de ces corpuscules le suc cellulaire, incolore au commencement prend une coloration violette. Dans les cellules adultes le pigment anthocyannique est dissous dans le suc cellulaire. L'observation de ces cellules, au début de leur formation, permet de suivre le processus d'élaboration de cette substance. A un tel stade du développement de la cellule on voit, tout d'abord, apparaître un cyanoplaste sphérique et très petit. Ce cyanoplaste, après son développement complet présente à sa surface des excroissances sphériques. Ces excroissances s'agrandissent et paraissent se multiplier par une sorte de bourgeonnement. Il se produit ainsi un assemblage de corpuscules sphériques.

On observe des cyanoplastes assez semblables dans les cellules épidermiques des anthères des fleurs de *Convolvulus tenuissimus* et d'autres espèces de *Convolvulus*.

Envisageons maintenant la question de l'hérédité. La couleur des fleurs est un des caractères héréditaires. Pour expliquer la transmission de ce caractère nous supposons qu'un gène qui sort du noyau se multiplie pour former des éléments spécialisés, qui produisent de l'anthocyane. Ce que nous avons supposé pour la formation de l'anthocyane nous pouvons le supposer aussi pour d'autres produits de l'activité de la cellule.

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SESSION 5

Jointly with Section FOR: July 17th, 2-5 p. m., See page 300

SESSION 6

July 17th, 7—11.30 p.m.

Chairman: Ö. WINGE

SUBJECT:

Studies in the USSR on the Nature of Hybrid Plants and Related Problems

This session was arranged particularly in order to give some members of the delegation from the USSR an opportunity to read their papers, which had not been announced before the Congress and therefore not been included in the programme.

I. E. GLUSHCHENKO (Moscow) *Hybridization of Plants by Means of Grafting*

1. The vegetative hybrids of the tomato obtained in our experiments and in the experiments of other followers of MICHURIN serve as evidence to the fact that the simple heredity typical for the vegetative reproduction can be transformed into the complex heredity characteristic of sexual reproduction as DARWIN, MICHURIN and LYSENKO taught and are teaching.

2. Experiments in the field of vegetative hybridization show the unsoundness of the chromosome theory of heredity which proceeds from the rule of cell from cell, nucleus from nucleus, chromosome from chromosome, and gene from gene.

The vegetative hybrids graphically show that as the living substance of the soma undergoes physiological changes, it forms, in the end, altered sex cells. There is no immortal germ-plasm, there are only the qualitative transformations of the soma which is capable of forming germ cells at a certain stage of this development.

3. There exists a similarity, a parallelism between the sexual and vegetative hybridization. It is expressed in the fact that any characteristic or any property can be transmitted

from one form to another both by the first and by the latter means. These properties become fixed in the seed generations.

4. At the same time there exists a difference between the two. A characteristic feature of the vegetative hybrids is that their type of segregation is different. Not only do individual plants differ from each other in their basic characteristics but a marked differentiation within one organism is observed. A mixed type of heredity is in general characteristic of the vegetative hybrids.

5. Another characteristic feature of graft hybrids is that they manifest dominance in another way. Plants with recessive properties often produce in the generation offsprings with dominant properties.

6. Crosses between the partners in the graft and their hybrids possessing recessive properties demonstrate that dominant properties may appear in the generation. This serves as evidence to the fact that certain properties that remain in the hybrid in the latent state and later on, under suitable conditions begin to develop in their generation.

7. Changes in morphological properties of the hybrids are connected with important anatomical transformations such as changes in the nature of cell structure, the appearance of various types of plastides.

8. Biochemical researches show that most

of the qualitative and quantitative indices of the second component of graft—the mentor—become manifest in the seed generations.

9. The frequently observed absence of visible changes during the year of graft does not mean that no definite qualitative changes have taken place in the germ cells of the plant. It therefore follows that the offspring of grafted plants always be studied even though no changes were observed during the year the graft was made.

10. It would be quite wrong to expect that as a result of the grafting the generation of the scion would always produce properties of the stock, or vice versa in the generation of the stock discover properties of the scion. The living matter is a process of development and never do any direct and immediate changes take place in a biological process. They develop through a long chain of transformations.

Alongside direct hybrid qualities (the presence of the characteristics in the generation of both parent forms) the vegetative hybrids possess a quality of forming new properties, i.e. of creating new properties that were present in neither of the partners in the graft. The extremely destabilized and labile nature of the forms which very often develop as a result of intraspecific grafts and particularly these between distant types serve as a prerequisite for this phenomenon.

K. S. SUCHOW (Moscow)

Directed Changeability of Phytopathogenic Viruses

The simplicity of the structure of virus nucleoproteids which combine the properties of homomolecular substances and living bodies opens significant possibilities for the study of the uncellular living substance.

The nucleoproteids of the viruses when reproduced in the protoplasm of plants belonging to different species undergo regular (and not fortuitous) heredity changes, the direction of which is determined both by the properties of the given virus strain itself and

by the specific physiological properties of the plant host. The study of such changes was conducted during passages of a simple virus strain of tobacco mosaic through the plants *Nicotiana glauca*, *N. sylvestris*, *N. longiflora*, *N. noctiflora* and *N. lancifolia*.

These examples graphically demonstrate the inheritance of new properties acquired by the proteins as a result of changes in their conditions of life. This confirms the principal postulations of MICHURIN's biology.

The properties of the virus nucleoproteids actually refute the metaphysical conceptions of the Morganists about the independence of the heredity of nuclear nucleoproteids in regard to the conditions of life of the organisms in whose protoplasm they are contained.

In these properties of the virus proteins are reflected the general laws governing the entire living matter, i.e. the dependence of development, heredity and its changeability in connection with the conditions of life, with the metabolic conditions.

The general biological law of development governing the entire living matter operates with equal strength in the most highly organized plants and animals and in the minutest particles of living substance exemplified by the viruses.

N. V. TURBIN (Moscow)

New Experimental Data on the Nature of Fertilization in Plants

Already CHARLES DARWIN pointed out that under the influence of facts of receiving vegetative hybrids the physiologists will have to alter fundamentally their point of view in respect of the process of fertilization. In the works of Professor LYSENKO and his followers the problem of fertilization has been revised on the basis of experiments in the field of vegetative hybridization. These works consider the sexual and vegetative hybridization as phenomena of the same order, similar in their physiological basis the substance of

which is the metabolic process (the process of assimilation and dissimilation).

The report contains MICHURIN's theory of fertilization and its consequences regarding the problem of metaxenias and of the significance of a great number of paternal gametes to be used in the process of fertilization. Experimental data of the author proving the possibility of producing hybrids inheriting properties of several paternal types participating in the joint pollination of the same maternal plant are cited. It is pointed out that MICHURIN's theory of fertilization serves as basis for a number of new effective methods in the field of selective seed-breeding that are widely used in the Soviet Union.

V. N. STOLETOV (Moscow)

Nature of the Hybrid Plants

The report contains certain points of principle in the teachings of MICHURIN - LYSENKO on hybridization.

1. The results from crossing the same pair of parents are never the same.
2. Nature does not know of the existence of any absolutely homozygotic organism.
3. There are no organisms in existence that are absolutely constant and that do not split.
4. Organisms that are beyond doubt hybrids are not necessarily subject to splitting.
5. The nature of the split of the hybrids is subject to the extent of biological relation of sexual cells which unite during the hybridization.
6. No complete split of the hybrid organism into purely parental types is observed.
7. "The hybrid is an indivisible organism. It does not divide into paternal and maternal possibilities of development. It possesses all these possibilities but develops in such a way as is best provided for by the specific conditions of the environment." (LYSENKO). Our experiments with the hybrids: winter types \times spring types showed that:
 - a) The nature of split proved to be dependent on the period of sowing.
 - b) The nature of the split of the hybrid offsprings of the third generation proved to be dependent on the time of harvesting the seeds in the second generation.
 - c) The nature of the split of the generations into winter and spring types proved to be strongly dependent on the time of seed formation in the preceding generation.
 - d) In cases of split in the hybrid generations there is no complete division into pure parental types.
 - e) The pure recessive, i.e. the winter type plant, started the formation of the dominant types, i.e. the spring type of plants.
 - f) The direction of the fermentative processes in the derivatives of the hybrid plants differs from corresponding processes of the initial parental types.
 - g) An increased activity of the fermentative processes is characteristic for the hybrid derivatives when compared to their parental types. Both the synthesizing and hydrolysing processes proceed more vigorously.

Discussion

Professor GLUSHCHENKO's report gave rise to a lively discussion which was characterized by the fact that due to language difficulties all questions had to be made in a written form. For technical reasons it was impossible to gather these questions and the corresponding answers and to publish them in these Proceedings.

It may be mentioned, however, that one of the most significant questions put to Professor GLUSHCHENKO was that of Professor QUINTANILHA, who requested an explanation, other than the chromosome mechanism, of the occurrence of a simple 2:2 segregation in cryptogams such as *Chlamydomonas*, *Coprinus*, *Neurospora*, and *Saccharomyces*. Professor

GLUSHCHENKO replied that he was unfamiliar with such material but that he was nevertheless prepared to maintain that such a segregation was a statistical phenomenon, and that sometimes 50 % of each type would occur, and different percentages at other times. Professor QUINTANILHA replied that this was not a question of statistics at all, for each 4-spored ascus or basidium in a heterozygote yields a 2:2 ratio. Professor GLUSHCHENKO said in conclusion that he did not intend to deny that at times the chromosomes were the carriers of heredity, but that there were other modes of inheritance as well.

Professor STOLETOV's report likewise gave rise to a discussion. His statement that "nature does not know of the existence of any absolutely homozygotic organism" occasioned the comment on the part of Professor MÜNTZING that "pure lines of barley are absolutely homozygotic and constant". In reply, Professor STOLETOV stated that "they may be constant at Svalöf, but if they come to another climate, as in Russia, this constancy will disappear".

In this connection, reference may be made to a number of papers which partly deal with this session and which have been published in *Hereditas*. They give a fuller account than this short summary of the contributions of the USSR delegates on this occasion.¹

With regard to the Russian assertion that a pear-shaped apple had been produced by

grafting apple and pear together, Dr. DARLINGTON stated that such new types had been known in England years ago, but that they were not the result of grafting but mutant forms.

This very lively discussion continued until midnight.

The Chairman stated that although he had many times encountered great differences of opinion in the scientific world, he had not previously known of two schools of thought being established on the basis of geographical boundaries, as the present MENDEL-MORGAN school in the West and the MICHURIN-LYSENKO school in the East. Divergent philosophical concepts should not be allowed to interfere with scientific results. Philosophy, the Chairman said, bears no relation to a natural science which is open to experimentation. In this respect, Russian scientists seem to be in a difficult position. Some months ago, when Professor ISAJEV was visiting Denmark, the Chairman asked him outright whether a Russian geneticist who arrived at results in agreement with Mendelian laws would be able to publish his results in Russia. Professor ISAJEV's reply was "no".

¹ LEVAN, A. and MÜNTZING, A. 1951. Correction of a report. *Hereditas* 37, pp. 293-305.

GLUSHCHENKO, I. E. 1952. Correction of a correction. Reply to Dr. ALBERT LEVAN and Professor ARNE MÜNTZING. *Hereditas* 38, pp. 370-376.

LEVAN, A. and MÜNTZING, A. 1952. Comments on Professor GLUSHCHENKO's "Correction of a correction". *Hereditas* 38, pp. 377-384.

SESSION 7

Jointly with Sections CYT and MYC: July 18th, 9 a.m. — noon, See page 424

SESSION 8

Jointly with Sections AGR, CYT and EXT: July 18th, 1—4 p.m., See page 174

SESSION 9

Jointly with Sections CYT, EXT and TPE: July 19th, 9 a. m. — 1 p. m., See page 277

SESSION 10

Jointly with Sections CYT, EXT and TPE: July 19th, 2 — 5 p. m., See page 277

SESSION 11

Jointly with Sections CYT and EXT: July 20th, 9 a. m. — 1 p. m., See page 219

MORPHOLOGY, MOR

President: A. J. EAMES

Vice-Presidents: J. T. BUCHHOLZ, K. ESAU, A. S. FOSTER,
H. VON GUTTENBERG, P. MAHESHWARI, F. MARKGRAF, V. MEZZETTI-BAMBACIONI,
P. MARTENS, H. PFEIFFER, R. WETMORE

Recorder: F. FAGERLIND

Vice-Recorder: M. RYBERG

SESSION 1

Jointly with Section FB: July 12th, 1—4 p. m., See page 551

SESSION 2

July 14th, 9 a. m. — 1 p. m.

Chairman: A. J. EAMES, Recorders: F. FAGERLIND and M. RYBERG

SUBJECT:

Structure of the Angiosperm Flower

I. SATINA and A. F. BLAKESLEE
(Northampton, Mass.)

*Periclinal Chimeras, a Tool in Determining
the Contribution of Germ Layers to Floral
Organs in Datura*

The shoot apex in *Datura* has 3 germ layers. Each can be affected by colchicine independently from the others. Combinations of 2n, 4n and 8n components gave various types of periclinal chimeras in which one, two, or three germ layers became polyploid. The floral apex as also the shoot apex, has three germ layers. Through chromosome number and cell size, individual layers and their resultant tissues can be labelled. The outermost layer (LI) forms epidermis. The second layer (LII) forms egg cells and pollen. The third layer (LIII), which is most frequently poly-

ploid, forms the central core of shoot and floral axis.

Development of leaf, sepal and petal is similar and depends primarily on the second layer. This supports view that sepals and petals are modified leaves. Epidermal cells produce inner tissue between adjacent petals and between sepals. Initiation of carpel primordia and early development of its wall, septa and placenta, as also that of the stamens, depend primarily on third layer. This suggests that carpel and stamen are axial and not foliar in origin. Styler wall develops from second layer and is foliar in nature. The third layer forms the vascular bundles. The transmitting tissue in style develops from first layer and is epidermal in origin. This fact enables the cross $2n \times 4n$, if female parent is periclinal with 4n epidermis and 2n second layer. Ovule

les initiate from innermost layer. Nucellus is formed by second layer which also gives rise to archesporial cell. Integument with its innermost layer—the endothelium, which encircles embryo sac—develops from first layer. The micropylar portion of ovular coat is formed by integument, the chalazal end by nucellar cells.

Our report is based on a detailed histological study of several hundred periclinal chimeras from seed treatment. A random sample of 100 seed-treated plants showed only 41 which were $2n$ throughout and 59 with branches which were chromosomally abnormal. Of the latter only 5 had the same chromosomal constitution in all branches.

It should be emphasized that chromosomal doubling occurs only in individual cells which are undergoing nuclear division. In consequence induced polyploidy generally results first in rough-leaved mixochimeras containing $2n$ cells and those with abnormal chromosome numbers such as $4n$, $8n$, and chromosome deficiencies. From such mixochimeras, branches may grow out in which all the cells of each layer are alike in chromosome constitution.

Discussion

A. S. FOSTER: Students of histogenesis welcome the introduction of colchicine-induced chimeras as a means of tracing cell lineages. But the speaker questioned the use of the term "germ layers" for the layers and core of tissue in the apex. The fluctuation in the rôle of cells derived from these layers would suggest considerable flexibility rather than precise determination. Comparative studies, using colchicine, on other members of the *Solanaceae* are highly desirable.

F. FAGERLIND: Dr. SATINA and Dr. BLAKESLEE have now shown that the *Datura*-carpel contains derivatives from layers deeper than those producing the leaves. RÖSLER found earlier that the wheat leaf is purely a derivative from the outermost layer of the growing stem-tip. But in chimeras of the same plant ÅKERMAN showed that the carpel really con-

tains derivatives from deeper layers. Earlier, I was not sure that the observation of RÖSLER was correct but now, after hearing Dr. BLAKESLEE, I feel that it is. I believe it is now proved that the carpel must be something else than a leaf or that it must be something more than a simple leaf and I think that the latter proposal is correct. A great deal of facts favour the opinion that the carpel is homologous with a leaf and with the corresponding axillary shoot-primordium which are fused together. Consequently, it should be homologous with the "scale-complex" in the Gymnosperms. In a paper dealing with the strobilus and flower of *Gnetum* and Angiosperms I pointed out earlier that the carpel must be something like that and that the stamen is either the upper fraction of a "scale-complex" or a whole "scale-complex." I believe this is in accordance with the findings in the paper now read.

Further contribution to the debate was given by E. BALL, A. W. BLAKESLEE and A. S. FOSTER.

F. MARKGRAF (München)

Morphologisch-phylogenetische Studien an Blüten von Cruciferen und Papaveraceen

MURBECK hatte in einer weitblickenden Übersicht alle Familien der *Rhoeadales* auf einen einheitlichen Typus zurückgeführt, indem er besonders das Androeceum untersuchte. Ein entscheidender Schritt dieser Vereinheitlichung ist aber der, dass dann die 4 Kronblätter der Cruciferen als gespaltene 2 mediane erklärt werden müssen. Dann würde das Cruciferen-Diagramm z. B. mit dem von *Dicentra* gut übereinstimmen. Hier fehlte jedoch bisher ein verbindender Typus, der in der Blumenkrone die Möglichkeiten zu beiden Richtungen enthielt und dadurch Merkmale eines gemeinsamen hypothetischen Vorfahren zeigte. Diesen habe ich in *Hypecoum* gefunden. Betrachtet man die medianen "Kronblätter" von *Dicentra*, die im Dienst der Bestäubung besonders ausgestaltet sind, genau, so sieht

man, namentlich bei *D. cucullaria*, deutlich je 2 seitliche Lappchen oder Spitzchen unter dem Mittelteil; die entsprechenden Petalen von *Hypecoum*, die gleichfalls eine Bestäubungsaufgabe haben, wurden von MURBECK wegen der Antheren-Ähnlichkeit ihres Mittelteils nur mit Staubblättern verglichen. Aber wichtiger ist es für unsere Frage, ihre seitlichen Lappen zu beachten, die wie bei *Dicentra* unter dem Mittelteil (zeitlich stark verzögert) entspringen, jedoch viel grösser sind und sich regellos decken wie die Kronblätter der Cruciferen. Es liegt nahe, diese ihnen homolog zu setzen mit Ausfall des Mittelteils. Von der anderen Seite her kann man nun nachweisen, dass bei *Sanguinaria* vollständige Kronblattsplattungen die Regel sind und dass diese sogar, wenn sie sich auf die Medianebene beschränken, genau den Cruciferen-Typus liefern, sogar mit unregelmässiger Knospendeckung der Seitenteile der medianen, dazu mit schwacher Aussackung von 2 Kelchblättern (wie bei *Hypecoum* und Cruciferen).

Einer solchen Deutung würde indes die Auffassung von EGGERS entgegenstehen, dass die medianen Kelchblätter später entstünden als die lateralen. Die Untersuchung sehr vieler Cruciferen-Blüten führte mich jedoch zu dem Ergebnis, dass die Entsprechung der medianen Perianthblätter bei den genannten Gattungen und Familien durch mehrere Eigenschaften wahrscheinlich gemacht wird; die Medianebene hat als ganzes einen zusammenfassenden Charakter: in ihr vollzieht sich die Zygomorphie (*Iberis*, *Teesdalea*, *Carponema*), gegen sie konvergieren die Ansatzpunkte der Kronblätter, namentlich in der Jugend, und daher ist auch in ihr die Knospendeckung der Kronblätter stärker als in der lateralen. Um aber auch ontogenetisch Gewissheit zu erhalten, regte ich Fräulein ALEXANDER an, die Entwicklung nachzuprüfen. Dabei entdeckten wir als Ursache des Unterschiedes die eigenartige Aufwölbung der Blütenachse der Cruciferen in der Medianebene, die bei den Papaveraceen fehlt. Fr. ALEXANDER lieferte nun folgenden Nachweis: die zuerst angeleg-

ten Sepala sind die medianen, die deshalb auch von Anfang an decken und deckend bleiben. Sofort nach ihrer Anlage beginnt aber die mediane Hebung, die sie über die seitlichen empor bringt, woher sie dann auch eine höhere, daher spätere Leitbündelversorgung bekommen. Dass diese Hebung ein Wachstumsvorgang ist, wird dadurch deutlich, dass die Zellen dieser Zone im Gegensatz zu ihren lateralen Nachbarn zu jener Zeit ein deutliches Streckungswachstum zeigen. — Die Petala bleiben ebenso wie die Seitenlappen von *Hypecoum* auffallend lange auf dem Primordialstadium stehen. Auch die Art der Bündelversorgung (seitliche Kelchblattbündel aus den Kronblättern abgegeben) ist bei *Hypecoum* dieselbe wie bei den Cruciferen. Diese seltsame Hebung erklärt nun zugleich auch, dass ein vielleicht erwünschter Übergangszustand — *Hypecoum*-Kronblatt mit reduziertem Mittelteil — bei Cruciferen nicht existieren kann: durch die Hebung werden von Anfang an die Seitenlappen auseinander gedrängt. Wenn sie krankhaft gestört ist, kann im Mediansektor ein ungespaltenes Kronblatt auftreten.

Durch all diese Beobachtungen ist erwiesen, dass die Cruciferen-Blüte mit der Blüte von *Dicentra* und *Hypecoum* wirklich echt homolog ist, dass demnach MURBECKS Theorie zu Recht besteht. Den Hypecoiden kommt mithin eine auffallende Ausgangsstellung innerhalb der *Rhoeadales* zu: von ihnen aus lassen sich die regulären und die dorsiventralen Fumarioideen ableiten und über *Eschscholtzia*, deren Kronblätter sich nicht selten spalten, auch die Papaveroideen. Von demselben Punkt gehen aber auch die Cruciferen aus und über *Cleome* die Capparidaceen (durch nachgewiesene Spaltung, MURBECK) und die Tovariaceen (mit vermehrten Gliedern in allen Blütenkreisen). Die Resedaceen zeigen an ihren Kronblättern Basalschuppen wie viele Cruciferen und Capparidaceen. Die Moringaceen und Bretschneideraceen klingen dagegen stärker an Leguminosen an als an Capparidaceen.

Bei der Frage, wo nun die Hypecoiden in entgegengesetzter Richtung angeschlossen wer-

den können, stösst man auf *Podophyllum*, das in Laub und Blüte grosse Ähnlichkeit mit *Sanguinaria* hat. Die lateralen äusseren Perianthblätter sind schwach sackförmig, die inneren oft verdoppelt und bisweilen unvollständig gespalten. Somit werden auf diesem Weg die *Rhoeadales* an die Berberidaceen mit ihren regelmässig alternierenden Quirlen von Blütenphyllomen angeschlossen, deren Blüten sehr klar aus gekreuzten Quirlen aufgebaut sind, und damit an die *Ranales*.

Discussion

In this discussion F. MARKGRAF, H. MELCHIOR and W. ZIMMERMANN took part.

V. PURI (Meerut)

Placentation in Angiosperms

It was well said that from time to time we should have a stocktaking of our botanical generalizations. Placentation in angiosperms is a good subject for the purpose. Not only is there some confusion regarding the use of different terms, but our knowledge about the various modes of placentation is rather superficial. During the past 60-70 years the study of floral anatomy has contributed substantially towards a better understanding of the flower. And it appears to the author that this offers reliable criteria for distinguishing and defining different types of placentation. Moreover, the ovular attachment was recently made the basis of a new system of classifying angiosperms into Phyllosporous and Stachyosporous. It will be worth our while to see how far, if at all, this division is well founded.

Regarding the terminology, most of the English, Continental and Indian authors distinguish, in some way or the other, between the placentation in monocarpellary, apocarpous gynaecia and that in multicarpellary, syncarpous ones. The former is generally called "marginal" placentation. Most of the American authors, however, do not distinguish it

as a separate category; they consider it as parietal placentation. This latter treatment is considered unsatisfactory and it has been suggested that, lacking a more suitable term, the placentation in monocarpellary and apocarpous gynaecia should be universally recognized as "marginal."

Again, the American authors do not appear to be unanimous on the use of the term "axile" placentation. While most earlier authors have used this term, others later replaced it by "axial" or by "central." It is suggested that the term "axial" (belonging to axis) is not so appropriate as "axile" (towards axis) and that it should be abandoned in favour of the latter. The term basal placentation should be restricted to the condition where the single ovule is situated in the center of the ovary.

The main types of placentation have been redefined on the basis of certain anatomical features which are considered to be more reliable than external form.

Referring to the correlation between the number of carpels and that of placentae, it is pointed out that, as a rule, the placentae equal the carpels. But in some cases, e.g. in the *Gramineae*, certain *Cucurbitaceae*, *Cappariaceae*, etc., the placentae are fewer than the carpels. This is believed to be due to some of the placentae becoming sterile.

Again, in a great majority of cases carpellary dorsals and ventrals, which give rise to placental strands, arise from the same "node," and it appears quite clear that the placentae are integral parts of carpels. In a few cases, however, it seems as if an "anatomical internode" exists between the origin of dorsals and placental strands. The present author is inclined to believe that this is probably due to the centripetal mode of growth—placentae being the last parts to develop—rather than to the independent status of the placentae.

Some special types of placentation are then discussed with particular reference to the condition met with in the *Rhoeadalean* families, and *Berberidaceae*, *Cucurbitaceae*, *Caprifoliaceae*, etc. It is maintained, as a consequence,

that there is no fundamental distinction between parietal and axile placentation.

Morphologically speaking, the placenta is believed to be carpellary. It is admitted that in the case of basal and free central placentation this may not always be quite clear, in so far as we may not have direct evidence to prove it, but comparative morphology leaves little doubt that it is the case.

Discussion

H. J. LAM: First the terms axile (=axillary) and axial (on the axis) are discussed. Axillary is probably the better term for a placentation in a 'corner.'

I do not think that all placentations are carpellary. To my mind there are no true carpels in stachyosporous groups. In that case, the placentation is basal or central. If there are carpels, the placentation is either marginal or laminal. Parietal is only a descriptive term without much ontogenetic significance.

P. G. OZENDA: Il est difficile aujourd'hui d'admettre sans réserve la généralité du schéma de VAN TIEGHEM suivant lequel les ovules seraient originellement des productions du bord des carpelles en relation constante avec les nervures marginales. Il semble au contraire qu'il puisse exister une certaine indépendance, en raison notamment des faits suivants:

a) Morphologie. Carpelles et placentas peuvent être en nombre différent dans une même fleur, comme V. PURI l'a lui-même rappelé. Divers cas de polymorphisme ont aussi été décrits, avec carpelles stériles.

b) Ontogénie. L'origine histologique du carpelle et des ovules est peut-être différente, les ovules dérivant d'une zone plus profonde de la fleur (BLAKESLEE et SATINA, PLANTFOL). Pour PAYER et pour HAGERUP, les carpelles sont appendiculaires, les ovules de nature axile.

c) Anatomie. Chez les Angiospermes primitives, les rapports vasculaires entre ovules et carpelles s'écartent souvent du schéma classi-

que. Chez les Magnoliales les ovules sont constamment en rapport avec la nervure médiane du carpelle, comme je l'ai observé dans les Magnoliacées et les Schizandracées et comme BAILEY et NAST l'ont constaté dans les Winteracées.

Further contribution to the discussion was given by J. DO AMARAL FRANCO, H. J. LAM, T. NAKAI and V. PURI.

H. BAUM (Wien)

Die Bedeutung der postgenitalen Verwachsung für das Verständnis des Baues von Karpell und Gynözium

Jedes Karpell besitzt einen Ventralspalt, der dadurch entsteht, dass die Dorsalseite des seiner Grundstruktur nach schlauchförmigen Karpells anfänglich viel stärker in die Länge wächst als seine der Achse zugewendeten ventralen Teile, wodurch der Karpellrand sehr stark in die Länge gezogen wird und schliesslich zwei parallel zu einander gerichtete Längsschenkel bildet, die durch das Breitenwachstum der Karpellspreite einander meist dicht genähert werden. Durch diesen Ventralspalt wird jedes Karpell in einen apikalen offenen Abschnitt und in einen basalen geschlossenen Abschnitt gegliedert. Da diese beiden Abschnitte miteinander in Korrelation stehen, ist man berechtigt, aus der Länge des Ventralspaltes auf den Anteil des offenen und des geschlossenen Karpellabschnittes zu schliessen, so dass man durch die Untersuchung des Ventralspaltes sich über den prinzipiellen Aufbau des Karpells orientieren kann.

Die Ventralspalten bleiben meist nicht zeitlebens offen, sondern verwachsen im Lauf der Ontogenese postgenital. Diese Verwachsung geschieht in der Weise, dass die Epidermiszellen der Spaltränder sich zunächst berühren, dann papillös werden, sich ineinander verzahnen und schliesslich durch tangentielle Teilungen in einen so festen Verband treten, dass die ehemalige Grenze mikrochemisch nicht mehr nachzuweisen ist.

Dieser charakteristische Verwachsungsvorgang manifestiert sich nun nicht nur an den freien Karpellen eines apokarpen Gynözeums, sondern ist auch an den miteinander verwachsenen Karpellen eines coenokarpen Gynözeums nachzuweisen, wodurch nicht nur die prinzipielle Übereinstimmung im Bauplan aller Karpelle bewiesen wird, sondern vor allem auch die Homologieverhältnisse des synkarpen und des parakarpen Gynözeums im Rahmen der Baueigentümlichkeiten des coenokarpen Gynözeums verständlich gemacht werden.

Sowohl das synkarpe als auch das parakarpe Gynözeum geht nämlich auf dieselbe ontogenetische Ausgangsform, und zwar einen nur peripher durch kongenitale Verwachsung zusammengehaltenen, im Inneren aber gänzlich unverwachsenen Karpellverband zurück, dessen ungefächerter Innenraum dadurch zustande kommt, dass die Ventralspalten der den Fruchtknoten aufbauenden Einzelkarpelle offen sind. Bleiben sie nun zeitlebens offen, resultiert ein parakarpes Gynözeum, verwachsen sie aber postgenital miteinander, kommt ein synkarpe Gynözeum zustande, dessen charakteristisch gefächerter Hohlraum demnach nur quantitativ von dem einheitlichen Hohlraum eines parakarpen Gynözeums verschieden und ihm daher homolog ist. Die Verwachsungs-

verhältnisse, die an den fertig ausgebildeten Karpellen und Gynözeen häufig nicht mehr erkannt werden können und deshalb trotz ihrer Wichtigkeit bisher nicht beachtet wurden, sind einwandfrei durch die ontogenetische Untersuchung zu klären.

Entgegen der Auffassung, dass der Bauplan des coenokarpen Gynözeums von dem des apokarpen Gynözeums prinzipiell verschieden ist, liefert also die vergleichende ontogenetische Beobachtung der postgenitalen Verwachsung an Karpell und Gynözeum den eindeutigen Beweis dafür, dass die Baueigentümlichkeiten des verwachsenblättrigen Gynözeums ausschliesslich durch die Eigenschaften der das Gynözeum aufbauenden Karpelle bedingt sind, umsomehr als in einzelnen Fällen auch die periphere kongenitale Verwachsung des coenokarpen Gynözeums durch eine postgenitale Verwachsung ersetzt werden kann, das coenokarpe Gynözeum sich also ontogenetisch sichtbar durch die Verwachsung freier Karpelle bildet.

Discussion

In this discussion E. BALL, H. BAUM, F. A. L. CLOWES, A. J. EAMES, A. S. FOSTER, C. W. WARDLAW took part.

SESSION 3

July 14th, 2—5 p. m.

Chairman: H. PFEIFFER, Records: F. FAGERLIND and M. RYBERG

SUBJECT:

Meristems and Differentiation of Plant Tissues

H. VON GUTTENBERG (Rostock)

Die Entwicklungsvorgänge im Vegetationspunkt der Wurzel

Die gesamte bisher vorliegende Literatur hat die Entwicklung des Wurzelvegetations-

punktes der Dikotyledonen nicht richtig erkannt. Das wesentliche dieses Vorganges besteht darin, dass im Zentrum des Vegetationspunktes keineswegs eine regellos angeordnete Zellgruppe liegt, auch nicht etwa die Initialen der Histogene unmittelbar aneinander stossen;

vielmehr tritt eine zentrale Schlusszelle auf, die sich unter Abscheidung von Segmenten immer wieder regeneriert. Diese von uns zunächst als Zentralzelle bezeichnete eigentliche Initiale der Wurzel kann somit einer Scheitelzelle gleichgestellt werden. Dass die Entwicklung aller Wurzelgewebe aus einer einzigen Zelle theoretisch möglich ist, wurde an einem Schema dargestellt. Die Scheitelzelle teilt sich nur selten, viel seltener als ihre Descendenten. Die Initialen des Periblems und die der Haube einschliesslich des Dermatogens werden häufiger erneuert, als die des Pleroms; dieses wird bei vielen Objekten wohl so gut wie ausschliesslich von bleibenden Plerominitialen aus erneuert. Es gibt aber genug Fälle, wo auch das Plerom sich von der Scheitelzelle her ergänzt (z. B. *Lupinus*, *Cucurbita*, *Acer*, *Althaea*). Alle bisher beschriebenen Entwicklungstypen lassen sich auf ein Grundschema zurückführen. Die beobachteten Verschiedenheiten beziehen sich nicht auf das Wurzelzentrum, sondern auf das Verhalten der Descendenten. Wenn sich diese in unmittelbarer Nähe des Zentrums in transversaler Richtung schnell vermehren, wird die Deutung der Bilder schwierig. Zartere Wurzeln der gleichen Pflanzen lassen aber auch dann das Grundschema deutlich erkennen. Die Teilungen der Scheitelzelle verlaufen unregelmässig, somit herrscht auch in ihrer unmittelbaren Nähe noch keine einfache Ordnung. Diese wird erst durch eine, kaum weiter erklärbare innere Gesetzmässigkeit geschaffen, die man folgendermassen charakterisieren kann: Jede neu gebildete Zelle entwickelt sich so, wie es ihrem Lageort entspricht. Am Pleromursprung strecken sich die Zellen achsenparallel, im Periblem verlängern sie sich in Richtung der periklinen Kurven. Die seitlichen Teile der Haube samt Dermatogen verhalten sich ähnlich, während der zentrale Haubenteil sich wieder achsenparallel streckt. Die ganzen antiklinen Reihen hängen genetisch zusammen, die periklinen Kurven entstehen durch synchrone, örtlich mehr oder minder übereinstimmende Querteilung der antiklinen Reihen.

F. A. L. CLOWES (Oxford)

The Promeristem of Roots

The promeristem is conceived as the smallest part of the apical meristem from which all future tissues are derived. It is equivalent to the apical cell of some Cryptogams, but differs in that none of its cells is normally totipotent. By analysis of cell complexes in periclinal and anticlinal planes it is possible to understand how the cells in different parts of the meristem divide and so see the shape and behaviour of the promeristem.

Examination shows that roots of different plants, and even of the same plant, may be of widely different architecture. In *Fagus sylvatica* the promeristem is shaped like an inverted cup. The initials of the plerome and the columella form the base of the cup. The initials of the periblem and the peripheral part of the root-cap form the sides of the cup and surround the columella. The initials of the plerome divide transversely only—the middle ones periclinaly and the outer ones anticlinaly. Their proximal derivatives divide both transversely and longitudinally. In some roots of *Fagus* the periblem initials and their immediate derivatives divide similarly to those of the plerome, but in large roots the outer periblem initials may divide both transversely and longitudinally and thus increase their number. In this case the proximal derivatives rarely divide longitudinally and there is usually an intermediate zone where neither the initials nor their derivatives divide longitudinally.

The initials from which are derived the epidermis and the peripheral part of the root-cap divide both transversely and longitudinally. The consequent increase in the number of potential initials is compensated for by a decrease in meristematic activity and by the sloughing of the outer cells. The columella initials and their derivatives divide transversely, but in large roots at certain stages the outer initials divide longitudinally also. When this happens the expansion of the plate

of initials results in the conversion of outer periblem cells to columella cells by alternation of the planes of cell expansion and division. Thus the promeristem is subject to changes brought about by the activity of its constituent initials. The changes are probably not automatic but are probably imposed by external conditions. The cells of the promeristem have the properties of initials by virtue of their position within the meristem and not by virtue of any peculiar inherent properties.

Discussion

A. S. FOSTER: Is there evidence that the embryonic endodermis functions as a "cambium" which is responsible for growth in thickness of the young cortex of roots?

F. A. L. CLOWES: Divisions in the inner periblem are not "cambium-like." The inner periblem has predominantly periclinal longitudinal divisions. The innermost layers of the periblem go on dividing longer than the outer layers, and the future endodermis has the latest periclinal divisions, followed sometimes by a series of anticlinal divisions.

A. J. EAMES: I agree with Prof. CLOWES' statement concerning the nature of the so-called "endodermis" of WILLIAMS. The confusion regarding the nature of the layer in question is largely a matter of terminology: this layer is a layer of meristem cells, not an endodermis; the true endodermis may be formed from this layer, but is not in any way identical with it.

C. W. WARDLAW: Which forces are responsible for the distinctive shape of the "Umeristem" and for maintaining it? Has the meristem been partly isolated from adjacent lateral tissues by appropriate incisions?

F. A. L. CLOWES: The shape of the promeristem may be a geometrical function of the shape of the whole apical meristem. Isolation of the promeristem has not yielded useful results because of the amount of callus formation in relation to the size of the isolated tissues.

Further contributions to the discussion were given by H. PFEIFFER and E. BALL.

K. A. CHOWDHURY and K. N. TANDAN
(Dehra Dun)

Meristems and Differentiations of Plant Tissues with Special Reference to Trees

Investigation of trees in tropical climates has shown that their growth activities (extension and radial growth) completely stop for at least two months of the year. As a rule, the extension growth precedes the radial growth and the gap between these two activities varies from 2 weeks to 3 months, irrespective of the fact whether the trees produce ring-porous or diffuse-porous woods. *Micheha champaca* L., an evergreen diffuse-porous tree, and *Melia azedarach* L., a deciduous semi-ring-porous tree, were studied from 1947 to 1949. Only the extension growth takes place during the first part of the growth-season, for about 2-3 months, then comes a period of no activity, lasting 2-4 weeks. The radial growth then starts for the first time and continues for 3-5 weeks, when the extension growth is again resumed. From then on both meristematic activities proceed simultaneously for about 3 months and finally stop for the season. The cessation of height growth may or may not precede that of the radial growth.

These observations differ considerably from those reported from Europe and North America. The extension and radial growth are said to begin simultaneously. A point to note here is that for temperate countries no data appear to be available as to the direction in which combined activity progresses in the current year's shoot.

An analysis of the data collected on Indian trees indicates that two distinct auxins are involved in the growth activities of a tree—one auxin for extension growth and the other for radial growth. Furthermore, these auxins seem to be capable of acting either separately or jointly, suggesting a possibility of their inter-conversion. Although the various stages

in the chemical reactions of these growth substances are not till now clearly understood, there are indications that they may not be so very different from what FILDES and others have recently reported about the growth in bacteria.

For further details see: Nature, London May 6, 1950.

K. ESAU (Davis, Calif.)

Developmental Aspects of Primary Vascularization

Two opposing concepts have been formulated regarding the relation of initial vascularization to the activity of the apical meristem. According to one, these meristems determine the course of vascular differentiation in the axis; the other is that vascularization at the apices might be influenced by the pattern established in the older parts of the axis. What is the actual course of primary vascularization? In the latter process 3 phenomena may be distinguished: 1) initiation of the vascular system in the form of procambium; 2) differentiation of the primary phloem and 3) of the primary xylem from the procambium. In the higher Tracheophyta the phloem commonly differentiates acropetally in the root and shoot; the xylem follows the same sequence in the root, but in the shoot it appears first in the leaf or near it and then differentiates acropetally in the leaf and basipetally in the axis. The procambium is described by some as differentiating acropetally from the older parts of the axis toward the apices, others visualize it, in the shoot, as progressing from the apex into the axis. This conflict in views partly results from lack of exact criteria for the identification of procambium. The conversion of the derivatives of the apical meristems into procambial cells is gradual and the decision at what stage of this conversion the cells represent procambium is a subjective matter. Then, it is technically difficult to reveal, in microscopic sections, the initial procambial pattern in its entirety: the procam-

bium deviates from the vertical course at the nodes; the internodes are extremely short near the apex; procambial tissue is continuously augmented through several levels of the axis; and the earliest procambial cells are not sharply differentiated from cells surrounding them. Available evidence suggests that procambial differentiation may follow more than one pattern. Perhaps the pattern of vascularization is determined not by the apical meristem alone and not by the mature axis alone, but by the interaction of the various physiological activities occurring in the different parts of the shoot. Variations in balance in these activities might cause changes in the course of vascularization.

Discussion

In this discussion E. BALL, F. A. L. CLOWES, R. GAUTHERET, H. PFEIFFER, F. M. SCOTT and C. W. WARDLAW took part.

W. RAUH (Heidelberg)

Das primäre Dickenwachstum der Dikotylen

Neue Untersuchungen haben gezeigt, dass das primäre Dickenwachstum nicht nur bei der Bildung der Monokotylen-, sondern auch der Dikotylenachsen, insbesondere der krautigen, eine grosse Rolle spielt, dass es hier aber in anderer Weise vor sich geht als bei den Monokotylen.

Der Vorgang des primären Dickenwachstums ist auf das engste verknüpft mit dem Erstarkungswachstum, worunter die periodische Zu- und Abnahme der Achsendicke im Verlauf der Längenentwicklung des Achsenkörpers verstanden wird. Es handelt sich um eine der Längenperiode der Internodien entsprechende Dickenperiodizität der Internodien, die darin zum Ausdruck kommt, dass der Achsenkörper in der vegetativen Phase im Verlauf der Entwicklung an Dicke allmählich zunimmt. Nach Erreichung eines Maximums, das mit dem Beginn der reproduktiven Phase zusammenfällt, verjüngt er sich wieder. (Bei-

spiel *Zea Mays*.) Die Sprossachse nimmt auf diese Weise die Gestalt eines Doppelkegels an. Diese Dickenperiodizität ist nun das Resultat zweier gleichzeitig ablaufender Vorgänge: 1. der Erstarkung des Vegetationspunktes und 2. des sich in der Nähe des Vegetationskegels abspielenden primären Dickenwachstums. Der Umfang des Vegetationspunktes erfährt im Verlauf der Achsenentwicklung eine beträchtliche Erweiterung (=Erstarkung), die einem Maximum zustrebt. Dieses wird am Übergang von der vegetativen zur reproduktiven Phase erreicht und entspricht dem Maximum der Achsendicke. Mit dem Eintritt in die reproduktive Phase nimmt bei Pflanzen mit terminalen Infloreszenzen das Volumen des Vegetationspunktes wieder ab. Hierin stimmen die Dikotylen mit den Monokotylen überein. In den rückwärtigen Teilen des Vegetationskegels spielt sich nun das auf Gewebeneubildung beruhende primäre Dickenwachstum ab, dessen Ausmass von der Erstarkung des Vegetationspunktes abhängt. Sein Betrag nimmt also in dem Masse zu, als der Vegetationspunkt erstarkt und umgekehrt hat dessen Volumenabnahme eine Abschwächung des primären Dickenwachstums zur Folge. Gesteigertes primäres Dickenwachstum findet seinen sichtbaren Ausdruck in der Ausbildung von Scheitelgruben, wie sie nicht nur bei den Palmen, sondern auch bei zahlreichen Dikotylen (*Plantago*, Kakteen, *Sempervivum*-Arten) festgestellt wurden.

Bei den Monokotylen nun nimmt das primäre Dickenwachstum seinen Ausgang von einer kambialen Zone, dem primären Meristemmantel, der nach aussen Gewebe produziert, wodurch schon auf der Höhe des Vegetationskegels eine beträchtliche Achsenverdickung bewirkt wird: kambiale Form des primären Dickenwachstums. Bei den Dikotylen dagegen ist der primäre Meristemmantel, obwohl vorhanden, nicht tätig und das primäre Dickenwachstum beruht auf Zellvermehrung in primären parenchymatischen Geweben, im Mark und in der primären Rinde. Er wird deshalb als die parenchymale Form des primären Dickenwach-

tums bezeichnet, wobei zwischen einer medullären (Verdickung des Markkörpers; die meisten Dikotylen) und einer kortikalen (Verdickung der Rinde; Kakteen, *Sempervivum*) Form unterschieden werden muss. Beides nun, die Erstarkung des Vegetationspunktes und die davon abhängige Steigerung des primären Dickenwachstums wirken sich im Erstarkungswachstum der Sprossachse aus, die demzufolge die Gestalt eines Doppelkegels annimmt. Da bei den Monokotylen nun sekundäre Verdickungsvorgänge fehlen (Ausnahme: *Draacaena*, *Aloë*, *Kniphofia* u. a.), wird diese Form zeitlebens beibehalten. Bei den Dikotylen dagegen liegt die Doppelkegelform nur vereinzelt vor (*Oenanthe aquatica*, *Sium latifolium*, *Trapa natans*), denn bei den meisten Dikotylen, auch bei den krautigen, setzt in Fortgang des primären Dickenwachstums in den rückwärtigen Sprossabschnitten sekundäres Dickenwachstum ein. Dieses kommt in der Ausbildung eines mächtigen Holzkörpers zum Ausdruck. Dadurch wird die vom Erstarkungswachstum veranlasste verkehrt-kegelförmige Gestalt der Sprossbasis teilweise oder vollständig „maskiert“. Im einzelnen müssen folgende Möglichkeiten unterschieden werden:

1. Erstarkungswachstum mit fehlender Maskierung.

Sekundäres Dickenwachstum fehlt vollständig. Der Achsenkörper behält in Übereinstimmung mit den Monokotylen seine verkehrt-kegelförmige Gestalt bei: *Sium*, *Oenanthe*, *Trapa*.

2. Erstarkungswachstum mit unvollständiger Maskierung.

Die vom Erstarkungswachstum veranlasste, aufwärts gerichtete Dickenzunahme wird von dem auf die Sprossbasis beschränkten sekundären Dickenwachstum nur teilweise ausgeglichen, so dass die Sprossachse auch äusserlich eine spitzwärts gerichtete Dickenzunahme aufweist (häufigstes Verhalten: *Brassica*-Arten, *Euphorbia pepus*, *Tropaeolum*).

3. Erstarkungswachstum mit vollständiger Maskierung.

Hierbei ist von einer verkehrt-kegelförmigen

Ausbildung der Stammbasis überhaupt nichts mehr zu bemerken, da das durch das Erstarkungswachstum resultierende Dickendefizit der basalen Region durch sekundäre Verdickung so kräftig kompensiert wird, dass die Achse gerade an der Basis ihre grössten Werte aufweist. Nur die verkehrt-kegelförmige Ausbildung des Markkörpers deutet auf ein kräftiges auf Erstarkung und primäres Dickenwachstum beruhendes Erstarkungswachstum hin.

Discussion

L. PLANTEFOL: Le très intéressant exposé de M. W. RAUH a le mérite de faire justice d'un schéma classique par lequel nous opposons pour nos élèves Monocotylédones et Dicotylédones, bien qu'il ne constitue qu'un cas particulier. Mais je dirai, au risque de me faire accuser de phytionisme, que j'aurais souhaité, que la tige ne fût pas totalement isolée et que nous ayons vu le développement foliaire progressif qui accompagne l'Erstarkungswachstum et l'explique sans doute partiellement. Je pense d'autre part que, bien que ce soit conforme à l'opinion généralement admise, l'accroissement en largeur des Cactées globuleuses n'est pas une forme corticale de la

croissance d'épaississement primaire, mais qu'il est surtout constitué par la soudure à la tige de bases foliaires charnues.

R. RAUH: Prof. PLANTEFOL schneidet das Problem der Kakteen an. Kakteen müssen noch eingehend untersucht werden, da bei ihnen sowohl medullares als auch kortikales Dickenwachstum vorkommt.

Further contribution to the discussion by H. PFEIFFER.

E. HEITZ (Basel)

Direct Measurement of the Grand Period of Growth of Consecutive Cells in the Root-Tip

It is shown that by direct measurement of consecutive cell series in the growth-zone of the living root-tip of *Melandrium album* and of the *Crepis* species the period of growth of each single cell in a cell row can be observed. The maximum of growth during 1-2 hours in a cell row is restricted to one or two cells only. The duration of the growth period of one cell is about 6 hours. The intensity of growth of a root-hair is greater than the maximum growth of a root-cell in the growing zone.

For further details see: *Experientia*, July 15, 1950.

SESSION 4

Jointly with Section CYT: July 17th, 9 a. m. — 1 p. m., See page 214

SESSION 5

Jointly with Section CYT: July 17th, 2—8 p. m.

Chairmen: G. F. L. TISCHLER, A. S. FOSTER and P. MARTENS

Recorders: A. LEVAN and F. FAGERLIND

SUBJECT:

Cytoplasm, Cellwalls, and Various Cell Constituents

H. H. PFEIFFER (Bremen)

Fortschritte in der Analyse des „capillary birefringent effect“ des Cytoplasmas

Der Effekt besteht darin, dass experimentell zum Fliessen gebrachtes Cytoplasma dabei

eine durch optische Anisotropie nachweisbare Orientierung seiner Leptonen zeigt. Mit dem Effekt verknüpft sind zwei weitere Phänomene, insofern die Fließgeschwindigkeit v/t des Cytoplasmas wie bei einer nicht-NEWTONschen Flüssigkeit in nicht-linearer Weise von

der Schubspannung abhängt und die absolute Viscosität mit variiertem Druck eine nicht-lineare Funktion bildet. An zum Fließen gebrachten Cytoplasma lässt sich bei möglichst achsenparallelem Strahlengange zwischen gekreuzten Nicols ein System farbiger oder bei monochromatischem Lichte hell-dunkler Interferenzstreifen nachweisen, welche parallel zur Capillarachse ziehen. Der optische Charakter ist negativ zur Fließrichtung, der Effekt also wohl auf die Lipoidkomponente der cytoplasmatischen Leptonen zu beziehen. Die Aufhellung steigt anfangs linear, dann langsamer als der Gradient der Fließgeschwindigkeit und nähert sich schnell einem Sättigungswerte (übereinstimmend mit Orientierungstheorie der Strömungsdoppelbrechung); bei Fortsetzen des Versuches nimmt ihre Intensität wieder ab (Überlagerung der Orientierungsanisotropie durch positiven photo-elastischen Effekt (Spannungsdoppelbrechung) oder Depolarisation von Leptonen). Mit grösserer Fließgeschwindigkeit können die cytoplasmatischen Leptonen durch Strömungsturbulenz desorientiert und die Intensität der Anisotropie herabgesetzt werden. Vorkommen von Ca-Verbindungen (vielleicht durch Sr, nicht durch Mg zu ersetzen), Separierung von orientiert die polypeptidischen Fadenmolekeln umgebenden Lipoiden, aber auch ein bestimmter Viscositätsgrad und hinreichende Intensität der Schubspannung scheinen erforderlich zu sein, um desorientierende Wirkungen der Brownschen Temperaturbewegung zu überwinden. Niedrige Temperatur während des rheologischen Experiments retardiert das Phänomen, durch Waschung mit Chloriden und teilweise andern Salzen der Alkalimetalle wird es in der Reihenfolge: $\text{NH} \gg \text{Na} > \text{K} \gg \text{Li}$ aufgehoben. Als Objekt brauchbar sind Cytoplasmotypen, welche gegen Verdauungseinwirkung von Pepsin und Trypsin resistent sind, aber nach Extraktion der Lipide leicht im Verdauungsversuch gelöst werden. Die rheologische Reaktion des Cytoplasmas ist genug definiert, um einen neuen Terminus für sie aufzustellen, da die „tropfige Entmischung“ E. ALBRECHTS für

gewisse Aspekte der Reaktion und die „Cytolysis“ für dieselben und andere Aspekte nicht gut gebraucht werden können, weil sie Interpretationen der cytoplasmatischen Konstitution einschliessen, welche in unsern Versuchen wahrscheinlich nicht realisiert sind. Da seit meiner vorläufigen Mitteilung auf dem internationalen Botaniker-Kongress in Amsterdam (1935) kein neuer Terminus vorgeschlagen wurde, spreche ich seit kurzem vom „capillary birefringent effect“. Das Phänomen lässt sich in Versuchsreihen anwenden zu einer neuen Bestimmung des Orientierungsgrades cytoplasmatischer Leptonen (vgl. H. H. PFEIFFER: Nature (London) 162, 419, 1948). Auch erlaubt der Effekt eine halbquantitative Bestimmung von Längendimensionen der Leptonen experimentell isolierten Cytoplasmas (unveröff. Vers.).

A. FREY-WYSSLING (Zürich)

Electron Microscopy of Cell Walls

In plant cell walls the electron microscope reveals a framework of cellulose microfibrils with an unexpectedly constant diameter of 250–300 Å. These are of general occurrence in angiosperms (wood, coleoptiles, root tips, root hairs) and algae (*Valonia*, *Spirogyra*). In fungi they are replaced by similar microfibrils of chitin (*Phycomyces*). X-ray studies permit the distinction of chitin from cellulose; in contrast to microchemical assertions these two wall substances never occur together in the same species.

Each microfibril consists of at least 2000 parallelized chain molecules, which are partly crystallized and partly paracrystalline. It is an important fact that the microfibrils never aggregate to form coarser strands, except in bacterial cellulose.

In the secondary wall (up to 95% cellulose, growth by apposition) of fibres, tracheids and sporangiophores, the microfibrils run parallel (parallel texture). The submicroscopic capillaries between them permit the circulation of liquids and the deposition of incrusting sub-

stances, such as lignin, cutin, and mineral substances.

In primary cell walls (less than 50% cellulose, growth by intussusception), the microfibrils have the same diameter as in the bulky secondary wall (exceptions with finer fibrils: pollen tubes, mosses both as gametophyte and sporophyte). They appear to be crossed (dispersed texture) and interwoven as in a fabric. It is difficult to understand how a texture consisting so to say of warp and weft expands. In the electron microscope two types of growth in area have been found: 1) tip growth with microfibrils originating in an amorphous mass (sporangiophore of *Phycomyces*). This is another case where microfibrils, somewhat thinner than the above-mentioned standard diameter, have been observed; 2) extension growth where the woven texture of microfibrils is loosened. The loosening may be caused by an increase of interfibrillar substances (pectins and hemicelluloses). The expanded areas are "mended" by the insertion of new threads, whereafter adjacent areas undergo the described loosening and readjustment at their turn. When the extension growth comes towards its end, the deposition of the secondary wall starts. We have found transition lamellae mediating between the dispersed texture of the primary and the parallel texture of the secondary wall.

Plant slimes have a loose frame of cellulose microfibrils as well, irrespective of the fact whether they are declared as cellulose, pectin or callose slimes in literature; there is merely a smaller proportion of cellulose in the last two categories. The slime layer of root hairs displays the most beautiful texture of such microfibrils, which are anchored in the primary wall.

Seemingly, there are two components in plant slimes: There is an extremely hydrophilic amicroscopic molecular gel, such as pectin or hemicelluloses which band many times their own weight of hydration water; this very soft gel is stiffened by a framework of submicroscopic cellulose fibrils, which procures rigid-

ity and elasticity as a mechanical support. In the series pectin slimes-cellulose slime-primary walls-secondary walls there is no fundamental difference of submicroscopic organization. It is only the amount of the interfibrillar hydrophilic gel dominating in the slime, that is gradually reduced to reach a minimum in the secondary wall.

W. W. VAROSSIEAU (Delft)

On the Use of the Electron Microscope in Wood Anatomy

The structure of solid woodblocks has been studied, making use of a new replica technique, developed in the Division for Electron Microscopy of the Technical Physics Department, Delft. The procedure of this method is as follows:

1. A print of a solid woodblock is made with alkathene (polyethylene) grade 20, at 115°C and at 2 atm. pressure.

2. A positive collodion replica is made of the alkathene matrix. As this replica cannot be prepared thin enough to be used directly in the E. M. two more steps are necessary.

3. An aluminium film of about 20 Å. U. thickness is evaporated in vacuo from all slides on the collodion print. In order to obtain a relief in the picture a gold manganin shadow cast is imposed on the aluminium film at an angle of 45°.

4. The collodion is dissolved in the condensing vapor of amylacetate.

The material examined comprises the following items:

1. Clear cut end surfaces and longitudinal surfaces of normal spruce (*Picea excelsa* Lk.) and pine (*Pinus silvestris* L.) blocks.

2. Spruce samples, decayed under laboratory conditions for a period of 3 months by *Coniophora cerebella* ALB. et SCHW. Strain Pless. (The loss in weight determined on half of the blocks varied from 23.3% to 32.3%.)

3. The cell wall structure in the line of failure in pine samples, compressed parallel to the grain.

So far experiments are done with "uncleaned" wood, which means that no chemical constituents (such as lignin) have been removed due to the preparation technique.

Conclusions:

1. The electron microscope may have a very limited application in problems of wood identification (pit structure).

2. Cell walls of decayed wood show white areas with typical constrictions. These areas precede a local breakdown of the wall. As these features are not observed in normal or mechanically damaged wood, they seem to be characteristic for fungal attack.

3. Changes of structure observed in the line of failure of mechanically damaged wood consists of a granular structure in the cell wall. This feature does not show in micrographs of normal and decayed wood and therefore seems to be characteristic for mechanical damage.

4. Micrographs within each of the subjects mentioned show mutual resemblance. However, obvious differences are noticed between the groups "normal structure," "decayed wood" and "mechanically damaged wood." Further investigation is necessary to determine in how far these differences are really characteristic.

W. SEIFRIZ (Philadelphia, Pa.)

The Effects of Narcotics on Protoplasm

(Motion picture)

F. M. SCOTT (Los Angeles, Calif.)

Plasmodesmata, Nucleodesmata, and Plastodesmata, and the Suberization of the Internal Surface of Plant Tissues

Living cells are interconnected by plasmodesmata. In the individual cell fibrillae, termed here nucleodesmata and plastodesmata, connect the nucleoplasm and the plastid stroma with the cytoplasm, and thus form a

continuous network, an integral part of the protoplasmic reticulum as a whole. The limiting membranes of nuclei and of plastids are perforate.

Plasmodesmata presumably function in the determination of cell shape. They occur in the branched cells of spongy mesophyll and of citrus rind albedo, in palisade elements, in differentiating spiral and pitted xylem elements and in latex tubes.

In the giant nuclei (diameter 100–200 μ) of the nucellus and endosperm of *Echinocystis macrocarpa*, nucleodesmata interconnect nucleoplasm and cytoplasm. Prior to ultimate resorption, the endosperm nuclei become lobed and nucleodesmata remain evident on the increased surface area. Nucleodesmata also occur in vegetative nuclei. They presumably function in material transport and are therefore significant in relation to plasmagenes and cytoplasmic nucleoproteins.

The term suberin here connotes a clear wall material resistant to strong sulphuric and chromic acids. Intercellular spaces are lined by suberin lamellae. Pellicles apparently similar, but more tenuous, line the inner surfaces of all cell walls examined. Suberin films appear first in the minute intercellular spaces of differentiating tissues, and thereafter keep pace with the expanding internal surface. Suberin may impregnate the entire cell wall. The ageing of a plant is thus accompanied by progressive suberization, intensification of fat metabolism. Internal suberization differs in degree in xerophytes, mesophytes and hydrophytes. In ephemeral flowers suberization is barely distinguishable, while in long lasting flowers it may be clearly defined. Xylem elements are lined with suberin. The inner surface of xylem and other elements may be micropitted, the protoplast surface correspondingly micropapillate, from which micropapillae micropasmodesmata may extend into the cell wall. Internal suberization must necessarily be considered in future discussions of solute transportation, transpiration, respiration and fat metabolism, and cell permeability.

K. HÖFLER (Wien)

Fluorochrome-Staining on Vital Cells

The fluorescence microscopy is one of the most modern methods of cell research. There is a primary and a secondary fluorescence. Staining by fluorochromes is more successful than common vital staining, since low concentrations may be used, and metachromasism produced by fluorochrome staining is brighter and more varied in colour.

A number of experiments can be seen on the thirty colour slides.

Following STRUGGER's example, dye-baths of varied pH were applied. By acridine orange of a weak basic reaction the cell saps of some objects, e.g. the inner epidermis of *Allium cepa* or the leaf epidermis of *Orchis maculata*, are stained red, whilst a weak acid reaction entails but an electroadsorptive staining of the cell walls. On the other hand, most other cells take on a green staining of the cell saps in the ultra-violet light, in the weak acid range as well as in the basic range. It is shown that the green colour is due to the chemical combining of the dye with some constituents of the cell sap, whilst a red colour is due to the kations of the dye being caught and accumulated in the vacuoles by the "trap mechanism."

Cell walls can be stained either electroadsorptively or by chemical combining. Only in the former case can they be discoloured by ionized salt solutions. "Alp-glowing" is a phenomenon caused by the disintegration of necrotic plasm, one phase perhaps richer in protein tinging the cell walls, the sheaths of the tonoplast or other particles to a bright red.

Nuclei become red or green by acridine orange. This, however, is no living test. The red-staining appearing above the IEP is an electro-adsorptive process, the green-staining, independent of pH, is based on chemical combining.

The electro-neutral Rhodamine B is, as found by STRUGGER, the most harmless dye.

It can neither stain the cell walls electroadsorptively, nor can it lead to a staining by ions in cell saps containing no constituents that accumulate the dye. Thus, in cells with such "empty saps" only the plasma is stained and the competition in accumulation can be demonstrated very nicely.—As to plastids it was recently observed that the storage capacity differs very much with different algae, e.g.: that of *Netrium digitus* is very great, whereas that of *Micrasterias* and others is quite small.

Coriphosphine is an excellent metachromatic fluorochrome introduced by HATTINGER. It is stored much stronger by the cell walls, like substantive dyes. But if cuts of *Allium* are later treated by Na_2CO_3 the coriphosphine is washed out of the cell walls, and there results a tonoplast-plasmolysis and a storage of the dye in the vacuoles with red radiation in the ultra-violet light.

Summarizing, we must admit that everywhere the undissociated and electro-neutral molecules are lipid-soluble and capable of permeating through the plasm, whereas the contrary is true for ions, which is the strongest support for the validity of the lipid-theory. We must realize, I think, that there is a continuous lipid-phase in the plasma reaching from the plasmalemma to the tonoplast.

P. DANCEARD (Bordeaux)

Sur la destruction du chondriome par l'acide acétique dilué et sa régénération dans la racine de Pin maritime

Nous avons montré qu'il était possible de détruire le chondriome dans les cellules des poils de Courge au moyen d'acide acétique dilué, tout en permettant aux cellules de survivre. Dans ces conditions le chondriome est régénéré (Le Botaniste, 31, 1942, p. 226).

Plus récemment nous avons montré dans diverses racines, non plus par la méthode vitale, mais en employant des fixations suivies de colorations, que le chondriome pouvait être complètement détruit dans les méristèmes

par certaines doses d'acide acétique, tout en laissant à ces méristèmes la faculté de survivre (Comptes Rendus Acad. Sc., Paris, 229, 27, 1950). Là encore le chondriome est rétabli dans les cellules en survie, apparemment au moyen d'une néoformation. Ces expériences apportent une démonstration du fait généralement méconnu que les mitochondries ne naissent pas uniquement de mitochondries pré-existantes mais peuvent également se former de novo au sein du cytoplasme.

Or nos résultats obtenus jusqu'à présent sur un petit nombre de plantes (Pois, Haricot, Lupin blanc, Courge) viennent d'être étendus à un nouvel exemple, la plantule de Pin maritime (*Pinus Pinaster*). Dans cette plante le chondriome et le plastidome peuvent être détruits complètement dans le méristème terminal de la racine par l'action durant 20 ou 30 minutes d'acide acétique à 1 p. 100, ou durant 4 h., de l'acide acétique à 1 p. 1000 sans empêcher la survie des cellules qui reforment après 24 heures un chondriome normal. La régénération du plastidome ne peut pas jusqu'à présent être affirmée.

R. A. BUVAT (Paris)

Les effets cytologiques de l'eau et le déterminisme de la forme des chondriosomes

Lorsqu'une cellule vivante est placée en milieu hypotonique, de l'eau pénètre dans le protoplasme, modifiant les propriétés et les structures de ses constituants. Dans certains cas, l'entrée de l'eau altère la matière vivante.

Nous avons obtenu le rétablissement de cellules de tubercules de *Cichorium intybus* qui, sous l'effet de l'eau, avaient subi des altérations, réputées irréversibles, telles que la vésiculation des chondriosomes et l'alvéolisation du cytoplasme.

En immergeant les cellules dans l'eau distillée, nous avons constaté successivement: l'activation passagère de la cyclose et le morcellement des chondriosomes («granulisation»); l'hypertrophie et la vésiculation de ces organi-

tes; puis, la réduction des mouvements de cyclose et la formation de longs chondriosomes; ensuite, ces derniers se morcellent en reproduisant des chondriosomes semblables à ceux des cellules normales. Les cellules sont alors «accoutumées» et peuvent survivre dans l'eau pure, pendant plusieurs jours.

Nous avons constaté que ces altérations sont comparables à celles que produisent de nombreux facteurs, physiques ou chimiques. Il semble qu'ils provoquent tous l'apparition d'eau libre dans le cytoplasme aux dépens de l'eau liée aux colloïdes vivants. Cette eau déterminerait notamment la vésiculation des chondriosomes, connue sous le nom de «cavulation». Elle serait également responsable des troubles de la cyclose, qui constituent un symptôme des plus sensibles de l'altération du cytoplasme.

Certaines préparations permirent de suivre, pendant une à deux semaines, les chondriosomes d'une même cellule vivante. En combinant les observations de cellules vivantes et de cellules fixées et colorées, nous fûmes amenés à considérer les chondriosomes comme des associations linéaires de granules qui, à l'état isolé, sont les mitochondries. Les mitochondries présentent une tendance naturelle à s'associer en chaînettes, constituant des bâtonnets ou des filaments (chondriocontes). Cette tendance est contrariée par les mouvements de cyclose. Lorsque la cyclose est accélérée; les chondriocontes se morcellent en mitochondries. Inversement lorsque la cyclose est ralentie, les mitochondries ont tendance à se réunir en chondriocontes. Les longs chondriocontes des cellules différenciées proviennent davantage de l'association des chondriosomes en série linéaire que de leur allongement. En laissant au repos des cellules à petits chondriosomes (2 à 10), nous avons obtenu l'association en longs chondriocontes (50 à 100), très souvent ramifiés tandis que la cyclose avait disparu. Celle-ci reprend sous le microscope éclairé, et provoque le démembrement des grands chondriocontes en éléments semblables à ceux des cellules normales.

Ces techniques permettent de se rendre maître de la forme des chondriosomes et de la modifier à volonté, entre certaines limites.

D. NEUGNOT (Dijon)

Deuxième contribution à l'étude cytochimique des cyanophycées

Dans une publication antérieure (Comptes Rendus Acad. Sc., Paris, 230, 1950 p. 1311), j'ai décrit surtout l'appareil nucléaire tel qu'il apparaît en appliquant la technique de ROBINOW et la technique à la ribonucléase. De nouvelles recherches, faites sur un plus grand nombre d'espèces et avec diverses techniques complémentaires (FEULGEN, hématoxyline) sont venues confirmer mes premières conclusions; en particulier, j'ai obtenu des figures beaucoup plus nettes en effectuant les colorations à l'hématoxyline après hydrolyse chlorhydrique. Ces recherches m'ont permis en outre d'apporter des précisions sur d'autres constituants cellulaires:

1) *Granules métachromatiques*. — Une coloration au bleu de méthylène ou au bleu de toluidine, succédant à l'hydrolyse chlorhydrique qui détruit ces granules, permet de voir souvent, se détachant à la surface de l'appareil nucléaire par une coloration plus foncée mais de même teinte bleue non métachromatique, des anneaux, entourant les emplacements qu'occupaient les plus gros granules: ils doivent sans doute être interprétés (DUCHI, 1946) comme une enveloppe des granules, formée par le corps central.

En utilisant la technique de GOMORI (1941) comme l'avait fait NOBACK pour les Levures, j'ai pu mettre en évidence la présence de phosphatase alcaline au niveau des granules métachromatiques; ce fait contribue à prouver, comme les essais d'EBEL et les miens que des métaphosphates, sans doute en liaison protéique, sont les constituants principaux de ces granules.

2) *Inclusions lipidiques*. — En appliquant aux Cyanophycées les techniques que C. VENDRELY emploie actuellement pour les cel-

lules animales, j'ai obtenu des résultats concordants avec les siens:

a) par fixation osmique, puis action de l'hématoxyline, on colore non seulement l'appareil nucléaire, mais encore de nombreuses granulations cytoplasmiques.

b) si on détruit l'acide ribonucléique par hydrolyse chlorhydrique avant coloration, l'appareil nucléaire est rendu plus net, mais le nombre des granulations cytoplasmiques colorées est réduit; dans les cellules animales, elles correspondent aux chondriosomes et grains de sécrétion.

c) si on détruit à la fois les acides ribonucléique et désoxyribonucléique par hydrolyse trichloracétique avant coloration, les seuls éléments qui se colorent sont quelques (3 ou 4) granulations. Dans les cellules animales, c'est le nucléole qui reste seul coloré. C. VENDRELY a montré d'autre part que l'hématoxyline présente une spécificité relative pour les lipides phosphorés, et que le nucléole ne se colore que très peu après délipidation. De mon côté, j'ai pu colorer les quelques granulations en question par la technique de ROMIEU qui donne une coloration spécifique des léci-thines: ces granulations auraient donc une analogie chimique avec les nucléoles.

3) *Glycogène*. — J'ai reconnu enfin par la technique de BAUER la présence dans la cellule d'inclusions formées de glycogène ou de polysaccharides plus complexes.

J. POLITIS (Athens)

Recherches cytologiques sur le mode de formation de l'acide chlorogénique chez les Composées

La propriété que possède la solution alcaline de l'acide chlorogénique de se colorer en vert en présence de l'oxygène a particulièrement attiré notre attention et, pour la répartition de cet acide dans le règne végétal nous nous sommes servis de la méthode suivante: Nous coupons les feuilles ou d'autres parties végétales à examiner en petits morceaux et nous les plaçons dans de petites tasses, en y ajou-

tant une solution d'ammoniaque à 1:5. Au bout de 10-20 heures nous examinons la solution ammoniacale. En cas de présence d'acide chlorogénique celle-ci devient verte et en présence de tanin elle prend une coloration brune ou rouge-brune.

Nous avons examiné un grand nombre d'espèces appartenant à 500 genres et 80 familles, parmi lesquelles nous avons trouvé 1100 espèces contenant une substance qui donnait les réactions de l'acide chlorogénique. Le but de la présente note est de communiquer les résultats de nos recherches cytologiques sur le mode de formation de l'acide chlorogénique chez les Composées.

En examinant sous le microscope les cellules épidermiques des fleurons de *Matricaria chamomilla* L. nous pouvons suivre la production de l'acide chlorogénique. Dans chacune de ces cellules, outre le noyau, on voit au commencement un très petit corpuscule sphérique, incolore, se colorant en vert sous l'influence des vapeurs d'ammoniaque, en bleu vert avec le bleu de méthylène, et présentant les caractères microchimiques de l'acide chlorogénique. En s'accroissant, ce corpuscule devient plus grand que le noyau et parfois il présente sur sa surface des protubérances sphériques. Ces protubérances s'engradissent et paraissent se multiplier par une sorte de bourgeonnement. Ces corps finissent toujours par se dissoudre dans le suc cellulaire, qui prend, sous l'action des vapeurs d'ammoniaque, une coloration verte due à l'acide chlorogénique. Nous avons aussi trouvé les mêmes corpuscules dans d'autres espèces appartenant à la famille des Composées.

Envisageons maintenant la question de l'hérédité. La présence de l'acide chlorogénique dans la plante est un caractère héréditaire. Pour expliquer la transmission de ce caractère nous supposons qu'un gène, qui sort du noyau, se multiplie pour former des éléments spéciali-

sés, qui produisent de l'acide chlorogénique. Ces organites spécifiques par lesquels s'élabore cet acide nous désignons sous le nom de chlorogonoplastes.

J. POLITIS (Athens)

Origine des vacuoles spécialisées

PFEIFFER a montré, depuis longtemps, que les vacuoles végétales pouvaient accumuler de colorants comme le bleu de méthylène à partir de solutions extrêmement diluées. Avec ce colorant nous avons obtenu une coloration perceptible des vacuoles des jeunes racines. Pour obtenir une coloration vitale du point végétatif, il faut détacher le sommet du méristème et le plonger dans une solution très diluée de bleu de méthylène. Au bout d'un séjour prolongé (6-12 h.) le colorant pénètre et donne une coloration vitale dans les cellules situées au sommet.

Nos résultats obtenus par la méthode des colorations vitales, permettent de montrer l'existence dans une même cellule de plusieurs sortes d'éléments évoluant en jeunes vacuoles. D'autre part WENT, KLERCKER, ILIUD, MANGENOT, BAILEY, GUILLERMOND ont révélé deux catégories de vacuoles dans les cellules d'un grand nombre de végétaux. Dans une même cellule on observe des vacuoles riches en tanoides et des vacuoles dépourvues de tanoides. Ces vacuoles spécialisées apparaissent de très bonne heure; leur origine n'a pu être précisée.

Nos observations sur des cellules renfermant de l'anthocyane nous ont conduit à supposer qu'un gène qui sort du noyau se multiplie pour former des éléments spécialisés qui produisent de l'anthocyane. Ce que nous avons supposé au sujet de la formation de l'anthocyane, peut aussi s'appliquer à d'autres produits de l'activité de la cellule (alcaloïdes, glucosides, tanoides etc.).

SESSION 6

Jointly with Section PB: July 18th, 9 a. m. — noon, See page 576

SESSION 7

July 18th, 2-5 p. m.

Chairman: K. ESAU, Recorders: F. FAGERLIND and M. RYBERG

SUBJECT:

Experimental Morphology

R. H. WETMORE (Cambridge, Mass.)
*Tissue and Organ Culture as a Tool for
Studies in Development*

The possibilities of the use of tissue culture techniques as an aid to understanding factors underlying growth and development in vascular plants have become very evident in recent years from the important investigations of WHITE, GAUTHERET and his students, NOBÉCOURT, ROBBINS, BALL, DE ROFF and others. Few successful attempts have been reported on the growing *in vitro* of mature plants from isolated apical meristems of stems. However, the results of BALL (1946) with *Lupinus albus* and *Tropaeolum majus* and LOO (1946) with *Asparagus* and *Cuscuta* showed that whole plants could be so grown. Recently, as an added technique to supplement surgical studies and physiological investigations on apical meristems, the author undertook a series of "in vitro" cultures of apices in the hope of obtaining significant information on the development of stems and their appendages.

The initial cultures were made of the apical meristems of *Adiantum pedatum*. Terminal pieces of 0.25 mm or less were placed on the standard nutrient agar employed by GAUTHERET (1942), which was supplemented by 2% dextrose and by naphthalene acetic acid in different concentrations, that of 5×10^{-8} and 10^{-7} proving most satisfactory. Growth was evident within the first few days. In two weeks new leaves were developing. In five months, several leaves on a rhizome were apparent and roots were well established. Except in their smaller size, the *Adiantum* plants appeared

perfectly normal. In eight months, several plants were placed in soil and at the present time give every indication of being well established and of becoming plants of normal size and morphology. Study of the structure of the rhizome indicates the stelar and extrastelar organization characteristic for this species.

When apices of the rhizomes of some of these plants grown *in vitro* were excised and cultured on a similar medium, the original results were duplicated. Indications are that normal growth and development can be duplicated indefinitely. In no single culture did one get juvenile leaves or abnormalities in external appearance or in internal organization.

Corresponding results have been obtained with such taxonomically widely separated plants as *Selaginella Willdenovii*, *Osmunda cinnamomea*, *Equisetum hiemale*, *Helianthus annuus* and *Curcubita texana*.

While variations in the medium prove significant, the effects of yeast extract, vitamin B mixtures, coconut milk, even the presence or absence of an auxin, are more quantitative than qualitative. In fact greater contrastive results are found from high and low concentrations of auxin than from any two of the above.

It is clear from these studies that the apical meristems, when supplied *in vitro* with proper mineral nutrients, with a carbohydrate source and with an auxin in proper concentration, can effectively demonstrate correlative growth and development. They give rise to normal, mature plants. That apices alone, supplied with mineral nutrients and sugar, are barely able to achieve this end is evident from our

studies. Auxin, over and above any which the apex may produce, has proven advantageous until leaves, or green stems, and roots, are well established.

Discussion

In this discussion E. BALL, R. GAUTHERET and R. H. WETMORE took part.

G. DEBRAUX et P. GAUVAUDAN (Poitiers)

Réactions des pièces florales isolées aseptiquement

Les pièces florales du *Lilium candidum* L., provenant de boutons floraux récoltés à différents âges (depuis 4 à 5 mm de hauteur jusqu'à complet épanouissement) peuvent être cultivées aseptiquement sur milieu nutritif sucré; elles se conservent pendant plusieurs mois et sont le siège d'une multiplication végétative comme les pièces foliaires elles-mêmes. Des boutons floraux entiers, des pièces périanthaires, des étamines, des ovaires, donnent naissance dans leur région basale à des cals volumineux, à des bulbilles, à des racines.

Discussion

G. MOREL: Étant donné qu'il est possible d'obtenir la culture indéfinie de *L. formosum* × *longiflorum* à partir d'embryons, je désirerais savoir, s'il est aussi possible d'obtenir la culture indéfinie des cals observés sur les pièces florales.

G. DEBRAUX: Les cultures indéfinies de tissus de cal doivent être possibles. Nos expériences sont récentes (Mai 1950); les premiers repiquages ont été effectués à la fin de Juin et, nous ne pouvons encore rien en dire.

Further contribution to the debate was given by E. BALL, G. DEBRAUX, M. ERNST-SCHWARZENBACH and C. W. WARDLAW.

C. W. WARDLAW (Manchester)

Comparative Morphogenesis in Pteridophytes and Spermatophytes by Experimental Methods

The recent renewal of interest in morphogenesis has resulted in intensified studies of the histological constitution, growth and formative activities of the shoot apex in all classes of vascular plants. An evident feature, long known and much discussed, is that these apices show great histological diversity; and descriptive terms which may be adequate for one apex, prove quite unsuitable for another. The inception of vascular tissue presents similar difficulties. Yet, notwithstanding this histological diversity, all shoot apices have much in common: physiologically and functionally they are closely comparable. The task, therefore, is to make meaningful this diversity of structure and, if it is possible, to produce general conceptions and descriptions which will apply adequately to all apices.

The problems of apical construction cannot be solved by the methods of anatomy alone, but progress along other lines may be possible: (I) experimental morphology; (II) physiological genetics; and (III) the development of new theoretical concepts.

One method of approach was to apply the same experimental treatment to very differently constituted apices to see if closely comparable or divergent organographic developments would ensue. Selected ferns and flowering plants yielded closely comparable results in each of the following experiments: (a) when the apical meristem was isolated by vertical incisions, with concomitant severing of the incipient vascular tissue; (b) when very young leaf primordia were successively removed, and (c) when various treatments of the apex intended to modify the normal positions of leaf primordia and their phyllotactic sequence were applied.

In the light of this experimental evidence the tentative conclusion is reached that however much the apices of flowering plants and

ferns may differ from each other anatomically and histologically, they show a very high degree of physiological and functional similarity.

The bearing of physiological genetics and related aspects on the problem of the apical meristem is also considered.

Discussion

A. S. FOSTER: There is great need, in all future histogenetic and experimental work on apices, to include broad investigations of root apices. This is particularly necessary because vasculature in roots proceeds acropetally without "causal" relationship with foliar appendages.

Further contribution was given by E. BALL.

G. CH. CAMUS (Pasadena, Calif.)

Histological Differentiation as Caused by Buds

Past works on woody cuttings and seedling fragments have demonstrated that growing buds induce histological modifications in subjacent tissues. However, in these materials only a study of cambial reactions is possible. By using the plant tissue culture technique and cultivating fleshy tissues which are able to regenerate organs *in vitro*, one is able to investigate both cambial and parenchyma alterations.

Extensive study was carried out on root pieces of *Cichorium intybus* L. var. placed on agar medium, both in a normal and inverse position. Observations on normally oriented pieces showed that the tissues subjacent to the regenerated buds undergo quite characteristic modifications. In the case of buds formed above the phloem, these modifications begin with the multiplication of parenchymatous cells. Later, cribro-vascular bundles differentiate, which are continuous with those of the buds. The structures develop then obliquely into the tissues, connecting finally with normal cambium of the fragment. Below this junction, the cambium begins to produce nu-

merous vessels connected with one or two roots, formed on the lower part of the fragment. Modifications appearing in vascular parenchyma were also studied.

Similar observations upon buds formed on the inverted pieces showed that in no case did the subjacent tissues undergo any modification. This demonstrated that the histogenic action is transmitted only in a leaf-to-root direction. Analogous experiments done on *Scorzonera hispanica* L. var. and *Crambe maritima* L. confirmed the above reported phenomena, which suggest that the buds behave like "organizers."

In order to obtain more conclusive results, buds were grafted onto tissue fragments. In this way it was possible to see that the histogenic action is able to cross the graft line and show up in the stock. Finally, graftings made by placing a piece of either cellophane or agar between the stock and the scion showed that modifications occur also across the permeable membrane. Thus, definitive proof of hormonal nature of the histogenic action was established.

Identification of the involved hormone was attempted by using different synthetic growth substances on tissues and by comparing the characteristics of their action to those induced by the buds. The conclusion was reached that indoleacetic acid secreted by buds is presumably the substance responsible for histological differentiation.

Discussion

In this discussion R. BOUILLENNE, K. ESAU, R. GAUTHERET and P. NOBÉCOURT took part.

E. BALL (Raleigh, N. C.)

Experimental Dividing of a Shoot Apex

Shoot apices of *Lupinus albus* L. were divided by microscalpel into six approximately equal parts. Due probably to unavoidable inequalities of the portions, there were differences in their regeneration. The largest

portions regenerated into normalized shoot apices and produced normal subadjacent shoots with dictyosteles. Those portions of the original apex that were below the minimum size for regeneration underwent vacuolation and ceased all growth. The portions that were apparently near the minimum size and cell number for regeneration grew into smaller than normal shoot apices. Approximately one-sixth of the shoot apex apparently constitutes sufficient meristematic cells to regenerate a functional shoot apex. The lateral or flank cells of the shoot apex do not appear to be irrevocably destined to produce foliar primordia, but may, if isolated in small groups and given proper environmental conditions, regenerate into a functional apex.

The early growth of the small shoot apex, before the formation of foliar primordia, resulted in the formation of a subadjacent suspended rod of procambium. Later stages of growth entailed the attachment of this rod of procambium to the subadjacent pre-operational procambium. The differentiation of this procambium appears to be basipetal.

The shoots produced by the small shoot apices were of smaller than normal diameter and are termed thin shoots. The rod of procambium beneath the small shoot apices matured into a solenostele or a protostele. Since this vascular tissue had been produced by the shoot apex before the formation of leaves, it was considered cauline. Of the several thin shoots produced as results of the operations, one that had grown forty-nine days was cut into serial transections from base to apex. From the base up through 8.7 mm of its length and below the position of attachment of leaves there was a solenostele usually with a very narrow pith. With the formation of leaves by the apex, the subadjacent procambium was a ring of bundles. The latter was attached upon the top of the solenostele. It was concluded that the formation of procambium by the shoot apex in these shoots was determined predominantly by the apical meristem since the original procambium bundles in a

ring did not determine the apex to form similar procambium, and finally, the rod of procambium that matured into a solenostele did not determine the apex to continue production of provascular tissue in a similar pattern.

Discussion

L. PLANTEFOL: En effet suivant le rapport de position entre les fragments aussi formés et la disposition phyllotaxique préexistante les divers fragments, même parfaitement égaux, peuvent avoir des potentialités différentes. Un secteur qui se développe en une tige feuillée peut soit réaliser le développement auquel il était conduit par sa position phyllotaxique, soit réaliser un phénomène de régénération.

Further contributions were given by E. BALL, O. DAHL and C. W. WARDLAW.

E. M. HERING (Berlin)

Veränderungen pflanzlicher Gewebe unter dem Einfluss minierender Insektenlarven

Minen sind Frassgänge von Insektenlarven in blattgrünführenden Geweben (Blätter, Stengelrinde) oder im Innern von der Epidermis. Sie werden von der Epidermis oder ihrer Aussenhaut nach aussen abgeschlossen. Es handelt sich um Verwundungen mit sehr feinen Werkzeugen (Mandibeln); die in Minen auftretenden Veränderungen sind grösstenteils Wundgewebe, ihre Besonderheit liegt im Abschluss der Wunde nach aussen. Dadurch bedingt herrschen im Minengang höhere Luftfeuchtigkeit und abweichende Temperatur vor. Es werden die an 86 Arten von Minen im Blatt, Petiolus und Stengelrinde beobachteten Verhältnisse geschildert.

I. Art der Veränderungen: 1. Kallus-Bildung ist die häufigste Form (Wundkork wurde nicht festgestellt). Die Form der dünnhäutigen, plasma- und chlorophyllverarmten Zellen wird oft durch das Lumen der Mine bedingt. Selten findet sich dichte Chlorophyll-Lagerung. Die erst runden Zellen sind selten gezipfelt, flachen sich unter Druck der Umgebung

ab und erscheinen im Umriss korkähnlich, wachsen häufig fadenförmig in einheitlicher Richtung. Sie tragen oft Protuberanzen, die als „Pektinwärtchen“ gedeutet wurden; meist sind sie wenig getüpfelt. Stark schlitzförmig getüpfelte finden sich bei Kallus, der sich im zerstörten Xylem bildete, so dass er tracheale Umbildung erfährt. Kalziumoxalat-Drusen fehlen immer. 2. Zellvergrößerung und -Vermehrung wird selten gefunden, beschränkt sich auf Minen in *Petiolus* und *Medianus*. Erste wird bei Grundgewebe-Zellen in Übergängen von Mine zur Galle gefunden, letzte besonders in der Epidermis, die durch Druck von Kallus herausgewölbt wird, durch Fortwirken des Reizes sich übermässig vergrößert und dann einfaltet. 3. Nekrosen und Digressionszonen isolieren den Minengang vom gesunden Blattgewebe. Nekrosen häufig in der Epidermis, wenn nicht Parenchymreste an ihr verblieben sind; Digressionszonen, aus Gewebetrümmern und nekrotisch gewordenen Zellen, mit Larvenexcrementen belegt, grenzen die Minen oft gegen das Blattparenchym ab, bilden sich auch im Kallus innerhalb des Xylems.

II. Ort der Veränderung: Umbildungen können sich in allen Geweben des Blattes finden, höherer Spezialisierungsstand verwundeter Gewebe setzt Umbildungsmöglichkeit herab. 1. Im Mesophyll des Blattes ist das Schwammparenchym häufigst Kallus-Produzent. Kallus wächst auch in Hohlräume zwischen Palisaden und drängt die Epidermis nach aussen. Palisaden bilden selten Kallus, erleiden aber Vergrößerungen und Formveränderungen. 2. Nur bei *Salix* zeigen Minen im Innern von Epidermis-Zellen Kallus, der sehr hinfällig ist. Epidermen über Minen enthalten Anthocyananreicherung, die sich auf benachbarte Partien der Palisaden ausdehnen kann. Bei *Salix* erfolgte Bildung einer eigentümlichen Verdich-

tungsschicht auf Parenchym unterhalb der ausmiierten Epidermis. 3. Fibrovasalbündel werden meist von der Larve gemieden, selten spezialisiert sich die Larve auf das Xylem, dessen teilweise Zerstörung üppige Kallusbildung von den Markstrahlen her bewirkt. Kallus kann Teile des Sklerenchymringes abdrängen und in sich einschliessen.

III. Ursachen und Wirkungen. Kallus ist nicht durch Aufhören des Gegendruckes bedingt; Wirksamkeit durch osmotische Kräfte beweist Üppigkeit des Kallus nahe den Leitbündeln. Chemische Beeinflussung erfolgt durch hohe Luftfeuchtigkeit in der Mine und sich zersetzende Exkremente. Vegetationsperiode und Art der Pflanze wie auch des Insektes fördern oder hemmen die Bildungen. Pressung durch Kallus ruft Herauswölbung der Epidermen, deren Einfaltung, und Verkrümmung und Verbildung befallener Blätter hervor. In der Nähe der Minen oft Umdifferenzierung des Zellinhaltes, der als Folge von Stauung der Assimilate dichter und trüber erscheint. Ausgehöhlte Epidermis kann Querteilung der Palisaden wie auch starke Kutinisierung der darunter liegenden Zellwände zur Folge haben.

IV. Bedeutung für die Pflanze. Die neuen Gewebe dienen nicht dem Stofftransport, nur der Wasserversorgung. Niemals handelt es sich um echte Zell- oder Geweberestitution. Die Mannigfaltigkeit der Gewebe ist bei allen Veränderungen in der Mine der Vereinfachung gewichen. Sie verwischen die Unterschiede zwischen Mine und Cecidium.

Discussion

In this discussion P. CHAMPAGNAT, K. ESAU, R. GAUTHERET, E. M. HERING and G. MOREL took part.

SESSION 8

July 19th, 9 a. m. — 1 p. m.

Chairman: R. H. WETMORE, Recorders: F. FAGERLIND and M. RYBERG

SUBJECT:

Embryology of Phanerogams

J. T. BUCHHOLZ (Urbana, Ill.)

Embryology of Gymnosperms

More than 50 genera of living conifers are known. The embryogeny of about 80% of them has been investigated sufficiently to provide some facts of importance in the embryogenies, yet many require more detailed study. It is a rule that the same pattern of embryonic development is found in all species of a genus, though closely related genera may follow the same pattern. However, *Podocarpus* is exceptional. This large genus includes many diverse types of embryogeny, but within the sections of the genus the same conditions prevail that are found between genera in other families. The *Podocarpaceae* that have been singled out and described as separate genera *Acmopyle*, *Pterosphaera*, *Dacrydium*, *Saxegothaea*, etc. have embryogenies that fit into the series shown by the different sections of *Podocarpus*; some that have similar proembryos differ with respect to cleavage polyembryony. Thus, the formula of embryogeny may be added to a critical taxonomic diagnosis of genera, remembering that several genera may sometimes have embryogenies that are essentially alike. All *Taxodiaceae* have cleavage polyembryony. Most *Tazaceae* have simple polyembryony. The *Araucariaceae* afford an example in which the entire family have the same type of embryogeny always with simple polyembryony. The family *Podocarpaceae* is characterized throughout, as far as known, by the presence of peculiar binucleate cells in the early embryo.

Comparisons have been made between coni-

fers and other gymnosperms. In past years, I have placed considerable emphasis on the question of the occurrence of cleavage polyembryony vs. simple polyembryony, which seemed to afford a basis of classification. A new proposal as an explanation of the possible role of embryonic selection resulting from cleavage polyembryony is based upon differences in the embryos having like chromosomes and genes when derived from the same zygote. Differences in these embryos are due to variations in the amounts of male cytoplasm, or substances diffused from the male, at the time of fertilization. Since there is no means of exact division of cytoplasm corresponding to that of mitosis at nuclear division the distribution of cytoplasm within the proembryo may vary considerably in neighboring embryo initial cells as soon as diffusion is prevented by the formation of cell walls. Differences in the amounts of male cytoplasm received by various embryonic units affect their vigor of growth during the ensuing episode of embryonic selection.

Experimental evidence on *Pinus ponderosa* indicates clearly that embryonic selection covers nearly 6 weeks, a relatively long period, during which most embryos disappear and the few that survive differ greatly in size. This takes place before differentiation of embryos into root, stem and cotyledons, in a very rapid growth covering only 10 days or 2 weeks in which the largest of the few surviving embryos in each seed completes its development. Embryonic selection is, therefore, primarily a form of cytoplasmic selection and growth vigor a cytoplasmic phenomenon.

Discussion

R. H. WETMORE: Is there evidence that the cytoplasm from the sperm takes part in the embryo formation? Does this male cytoplasm have distinct staining or other characteristics by which it can be recognized?

J. T. BUCHHOLZ: There seem to be several morphological conditions in conifers which show the effect of male cytoplasm, expressed in different ways, e.g., the long narrow archeogonia found in *Podocarpus spicatus*, *P. andinus* and *Sageothæa*, in which the embryo develops with simple polyembryony. In these the four nuclei of the proembryo must migrate over a long distance to reach the other end of the egg. In this phase of development the substances diffused from male cytoplasm must also travel this distance, independently.

A. J. EAMES: In *Araucaria Biduilli* apparently all the cytoplasm entering into the embryo is male. This condition might perhaps support Dr. BUCHHOLZ's theory that an unequal distribution of male cytoplasm in the rows of proembryonic cells might be related to the development of cleavage polyembryony, since in the *Araucariaceae* there is only simple polyembryony.

J. T. BUCHHOLZ: It would seem to be entirely consistent with this idea.

Further contribution was given by G. F. L. TISCHLER.

A. CHIARUGI (Pisa)

Polyploidy in the Female Gametophyte of Flowering Plants

One of the most outstanding features in the construction of the female gametophyte (embryo sac) of angiosperms is the central diploidization process, which is, in the normal type, accomplished by fusion of polar nuclei into the secondary nucleus of the embryo sac. Such a phenomenon appears to be the reaction to a dehydration, occurring in the middle zone of the embryo sac according to a kind of gradient, starting from the micropylar and

chalazal poles, to be regarded as the zones of food supply to the embryo sac.

Polyploidy of central nucleus in the embryo sac is to be regarded as a stronger water request in a zone where the water deficiency and need is greater.

The existence of the above gradient is also evident in the 12-nucleate *Pyrethrum cinerariaefolium* type, characterized by a polarization $1+(2)+1$ (MARTINOLI) and in the development of endosperm in *Pyrus malus* (WANSCHER).

The leading motive of polyploidization of the embryo sac is accentuated in those types of development where many polar nuclei fuse in the centre of the embryo sac (*Penaea*, *Plumbago*, *Peperomia* etc.) as well as in others when a precocious fusion of the three chalazal megaspore nuclei (*Euphorbia dulcis*, *Plumbagella*) takes place.

The above phenomena are further accentuated by the double fertilization and formation of triploid endosperm, the polyploidy of which appears to be an efficient mechanism for its function as metabolic intermediary between the old and the new sporophyte. Also the irregular polyploidy of the endosperm in gymnosperms has an identical significance.

The polyploid nucleus lessens the lowering of the freezing point of nuclear sap and lowers the osmotic pressure by its higher ability to absorb water. By such a mechanism the haploid generation corrects its conditions of physiological inferiority in regard to the diploid tissue in which it is immersed.

Polyploidy in the haploid generation finds its parallel in the recent demonstration of polyploidy in differentiated tissues possessing a high metabolic activity, as revealed by experimental mitosis stimulation.

Discussion

J. T. BUCHHOLZ: I have been wondering about the physiological effect of binucleate (or multinucleate) cells, as found in nutrition tissue (tapetal cells, multinucleate cells of

gymnosperm prothallia etc.). Would a binucleate cell (nuclei=2) function similarly to a cell containing a 2n nucleus—would the effect be the same when the nuclear material is in 2 parts, as when the two are combined in a single 2n nucleus?

P. MAHESHWARI: Question 1: If the fusion of the polar nuclei in angiosperms is designed to correct the physiological inferiority of the endosperm in relation to the diploid tissue in which it is immersed, how would you explain the condition in the *Onagraceae* where the embryo sacs are four-nucleate and there is no polar fusion?

Question 2: Concerning the statement that the fusion of the polar nuclei is a reaction to a dehydration phenomenon starting from the micropylar and chalazal poles, is it based on some experimental evidence or is it only a hypothesis?

A. CHIARUGI: Reply to prof. BUCHHOLZ: the author has observed that the gametophytes where the two polar nuclei do not fuse, degenerate more easily than those where the polar nuclei fuse.

Reply to prof. MAHESHWARI: 1) This is an exception. *Onagraceae* is a family at the end of a phylogenetic line. 2) No, it is based on observations especially on the development of the gametophyte in *Pyrethrum cinerariaefolium* and in endosperm of *Pyrus malus*.

P. MAHESHWARI (Delhi)

Embryology of Angiosperms: Its Aims and Objects

Research on angiosperm embryology may be said to comprise three more or less distinct disciplines. The first, or descriptive embryology, in which the aim has been to uncover the chief facts regarding the development of the pollen and embryo sac and the processes of fertilization and seed formation, may be said to have reached its culminating point in 1898 with the discovery of double fertilization. The second, or comparative embryology, in

which interest has centered on an evaluation of embryological data for improving the existing schemes of classification, began in the present century. The third, or experimental embryology, is the latest and may still be said to be in a stage of infancy; America, Sweden and Germany are the leaders in this field.

While contributions such as those of BAMBACIONI (1928) which resulted in the discovery of the *Fritillaria* type of embryo sac and of GUSTAFSSON and FAGERLIND which have led to a clarification of our understanding of apomixis are of great value and interest, it is not likely that we shall have many outstanding discoveries in descriptive embryology, unless a technique is evolved for the study of living pollen tubes and embryo sacs. On the taxonomic side embryology has rendered considerable aid in reorienting our ideas in the solution of many taxonomic problems (mention may be made of SAMUELSSON's work on the *Empetraceae*; SCHNABF's on the *Liliaceae*; and NEUMANN's on the *Cactaceae*), and we may reasonably hope to look forward to further contributions along this line for a correct understanding of the systematic positions of many doubtful genera.

Of greatest interest in future will be the newer field of experimental embryology, where embryology comes in intimate contact with physiology and genetics. Storage of pollen; increasing the germinating capacity of pollen; inactivation of incompatibilities caused by defective pollen tube growth; embryo cultures; stimulation of the unfertilized egg to form a parthenogenetic embryo; and the chemical induction of adventive embryony are topics of great theoretical as well as practical interest. A small amount of progress has been made in some of these directions but a great deal remains to be done. The solution of these problems needs the joint efforts of embryologists, cytologists, geneticists and physiologists.

Discussion

In this discussion A. ERNST, P. MAHESHWARI and G. F. L. TISCHLER took part.

G. HARLING (Stockholm)

On the Embryo Sac Development in the Genus Anthemis

The formation and development of the megagametophyte have been studied in the following *Anthemis* species: *A. altissima* L., *austriaca* JACQ., *rigescens* WILLD., *tinctoria* L., *arvensis* L., *maritima* L., *peregrina* L., *ruthenica* BIEB. and *Cotula* L. All the species studied have tetrasporic embryo sac development. A number of tetrasporic development types have been found, all of which are connected by transitional forms. The organized embryo sac can contain 4-12 viable nuclei. According as four, three, two or one coenomegaspore-nuclei participate in the embryo-sac formation, the embryo sac is termed eutetrasporic, pseudotrisporic, pseudobisporic or pseudomonosporic. The tetrasporic embryo sac development in *Anthemis* is apparently always 2-phasic. Earlier statements as to the existence of a 3-phasic development are probably due to misinterpretation. *Ormenis mixta* (L.) DUM. has previously often been regarded as belonging to the genus *Anthemis* (= *Anthemis mixta* L.), although it differs greatly from all other species of this genus. The embryo sac development in *Ormenis mixta* follows, however, the normal type. The gulf between *Ormenis* and *Anthemis* is consequently further widened.

M. ERNST-SCHWARZENBACH (Zürich)

Development and Flower Biology of Elodea Species and their Hybrids

In his classical research on sex determination STRASBURGER (1910) tried to make tetrad analyses of *Elodea canadensis*. The pollen grains remain joined to tetrads so that it is possible to put only one pollen tetrad on the stigma of each female flower and thus to analyse, by the seeds produced, the mode of determination of sexual and other characters. STRASBURGER's work was not successful: he got only 1-2 seeds per fruit. WYLIE, too,

wrote in 1904 that only 1-2 pollen grains of each tetrad germinate. SANTOS (1924) measured the pollen grains and found that the tetrads consist of two smaller and two larger pollen grains, a size-difference referred to the difference of chromatin content between X- and Y-chromosomes.

Our self- and cross-fertilizations with *Elodea canadensis* from the St. Lawrence river and from Switzerland and with *Elodea occidentalis* gave a rather low fertility, which was not lower in crosses than in selfings. The compatibility is good, but the female fecundity (number of ovules per ovary) is very low.

Research on the development of the pollen, pollen measurements and pollen germinations proved that the low fertility is neither cytologically nor genetically but purely physiologically determined. The difference in size of the pollen grains, asserted by SANTOS, is not a real one. The fertility is determined solely by physiological conditions of pollen germination. Pollen grains of the closely related genera *Lagarosiphon* and *Hydrilla* on stigmata of *Elodea* germinated better than pollen of *Elodea*, but hybridizations of different genera have never produced seeds.

Discussion

P. MAHESHWARI: It is interesting that ordinarily only two pollen grains out of the quartet germinate in *Elodea*. The situation seems to be comparable to that reported by MAGNUS (1913) in *Podostemon* where the pollen grains occur in pairs and only one member of the pair is capable of germination.

A. RUTISHAUSER (Schaffhausen) und

H. R. HUNZIKER (Zofingen)

Zur Zytologie des Endosperms

Da die Zytologie des Endosperms an Schnittpräparaten oft nur schwer untersucht werden kann, wurde versucht durch Anwendung der HERTZ'schen Nuklealquetschmethode zu besseren Resultaten zu gelangen. Es hat

sich gezeigt, dass sich das Endosperm vieler Pflanzen nach Hydrolyse in n HCl leicht aus dem Nuzellus herauspräparieren lässt. In Quetschpräparaten isolierter Endosperme können die Chromosomen exakt ausgezählt werden.

Die ersten Ergebnisse dieser Präparationsmethode zeigen, dass das Nährgewebe aller bisher untersuchten sexuellen Ranunculaceen (*Ranunculus bulbosus*, *acer*, *repens*, *Delphinium Ajacis* und *Nigella damascena*) triploid ist. Die Endospermmitosen der Liliaceen *Lilium*

regale, *candidum*, *speciosum*, *Henryi* und *Fritillaria imperialis*, deren diploide Chromosomenzahl durchwegs $2n=24$ beträgt, weisen dagegen 60 Chromosomen auf. Die Endosperme dieser Pflanzen sind also, wie nach den embryologischen Untersuchungen von BAMBACIONI und COOPER zu erwarten war, pentaploid. In einigen Endospermen von *Lilium candidum* fanden wir indessen auch Mitosen mit 120 Chromosomen, bei *L. Henryi* ferner in einem Falle auch die hexaploide Chromosomenzahl $6n=72$.

SESSION 9

July 19th, 2—4 p. m.

Chairman: J. T. BUCHHOLZ, Records: F. FAGERLIND and M. RYBERG

SUBJECT:

Various Papers

F. J. DE ALMEIDA (Sacavém)

Morphological and Physiological Anomalies in Olea europaea L.

The author observed the following phenomena and vegetative modifications induced by environmental and physiological conditions in *Olea europaea* L.: a) differentiation of adventitious roots, favoured by an increase of heat and moisture, on swellings of the trunks or in the stem nodes of young plants; b) reduction in the relation length/width of the leaves; c) decrease of the angle of divergence of the leaf and appearance of fasciation cases in leaves and branches, probably influenced by the moisture and nitrogen content in the soil; d) ovule competition, leading to total abortion or to the development of two seeds, the drupaceous fruit taking a regular shape, contrary to the typical asymmetric fruit, due to seed evolution and inflection of the ovary sept; e) fruit-setting directly on the trunk; f) terminal instead of axillary flower and fruit-setting; g) spring fructification simultaneously with

normal flower-setting; h) exceptional phenomena of flower-setting in branches less than one year old, fruit-setting in autumn being thus patent in branches of two different ages.

These phenomena are influenced by physiological conditions of nutrition, and have a tendency to occur following years when accidental factors hinder the fructification.

F. MAEKAWA (Tokyo)

Origin of Stipules — A New Hypothesis

All hypotheses on the morphogenic significance of leaves assume that the stipules belong to the lowest part of a leaf blade. Here, let me suggest another hypothesis—that one of the stipular origins, at least, is a synthetic combination of two different kinds of leaves. I do not, however, venture to condemn as quite untenable hitherto acknowledged views.

As an illustration of my hypothesis, let me quote the case of '*Quercus acuta*.' It has buds, consisting of many imbricated scaly leaves arranged in 1/5-phylloclaxis. All those leaves

are arranged spirally and separated by the same distance. But in the upper part, there occurs some slight modification of the distance between some of two adjacent leaves. For example, the distance between the 20th and 21st leaves becomes slightly smaller, whereas that between the 21st and 22nd gets slightly greater, and for the following two a little shorter than in the first case, etc. Therefore, the distance between two leaves is alternately shorter and longer, until in the former case it diminishes to zero, *i.e.* in the later stage of modification, the last two approaching leaves combined into one set, with longer distance between the two nearest sets. These modifications are, however, so continuous that all the leaves can be classified into one class, the so-called S-class leaves.

Further up, we can find a small protuberance inserted between two S-class leaves in the set. Accordingly, as these protuberances appear towards the upper end they look more like normal leaf blades, while the S-class leaves are narrower and finer in texture. The leaf-blades are newly originated and come to be inserted between, but are not the transformation of, S-class leaves; therefore they may be called F-class leaves.

A set of SFS has the same arrangement as a typical leaf with stipules. It is clear that these stipules are not the differentiated basal part of a leaf, but only the synthetic result of two different kinds of leaves among which the previously existing leaves are transformed into stipules and are under the influence of the newly formed leaves. This process of transformation is a new form of stipular origin, which we may call the synthetic origin of stipules by means of insertion.

Discussion

A. S. FOSTER: The author is apparently not aware of several 19th Century hypotheses according to which stipules should be regarded as organs distinct from their associated "leaf." But the evidence from ontogeny and vascular

anatomy, I think, support the belief that stipules are basal modifications of leaves and not a separate category of organs.

G. DEBRAUX (Poitiers)

La feuille isolée en survie.

Réactions histologiques et anatomiques

Les feuilles de la plupart des espèces végétales survivent à l'état isolé pendant des temps variables. Leur conservation et leur survie sont soumises à des conditions de milieu particulières à chaque espèce. Au cours de la survie, il peut apparaître dans la feuille isolée des tissus qui n'existent pas dans les conditions normales de vie du végétal. La polystélie, rare chez les Angiospermes, peut être obtenue expérimentalement et à volonté dans le pétiole et les nervures des feuilles isolées de certaines espèces. Dans les espèces chez lesquelles le système vasculaire du pétiole et des nervures est en forme de couronne, les cellules des rayons médullaires se divisent par des cloisons tangentielles et constituent un cambium interfasciculaire dont les éléments se différencient en bois et en liber; dans les espèces chez lesquelles le système vasculaire du pétiole et des nervures est en forme d'arc, on assiste toujours à l'apparition d'un méristème supplémentaire conduisant à la production d'une plage de fermeture dans la région ventrale de l'arc fasciculaire; ces modifications histologiques contribuent dans les deux cas à transformer la structure à symétrie bilatérale de ces organes en structure rayonnée de tige. Les observations concernant les espèces pourvues de liber interne apportent un argument en faveur de la théorie défendue par LIGNIER, BARANETZKY et PERROT et montrent que le liber interne représente un système vasculaire indépendant, incomplet, mais susceptible d'être complété par la différenciation ultérieure de vaisseaux ligneux. Toutes ces modifications histologiques et anatomiques sont en relation étroite avec la teneur des organes végétaux en

auxine naturelle dont le transport est perturbé par les conditions de vie nouvelles; ceci permet de supposer que les formations histologiques surnuméraires qui se produisent dans les tiges chez certaines familles végétales et que les botanistes considèrent comme des anomalies de la croissance (faisceaux vasculaires surnuméraires de l'écorce, du péricycle, de la moelle) sont déterminées par la réalisation à un moment donné et en certains points, chez ces espèces, d'une concentration convenable d'hormones de croissance, due aux conditions particulières de synthèse ou d'absence de conduction ou de destruction. Il est vraisemblable que les hétéro-auxines agissent sur le métabolisme des sucres et contribuent à déterminer en un point donné une concentration en sucre soluble suffisante pour produire le déclenchement des caryocinèses. L'analogie qui existe entre les formations observées dans les feuilles isolées en survie et celles qui apparaissent dans les organes végétaux parasités par les Insectes ou les Acariens (Cécidies) permet de conclure que les parasites sécrètent des substances à action hormonale.

A. S. FOSTER (Berkeley, Calif.)

Venation Patterns in the Leaves of Angiosperms, with Special Reference to the Quinaceae

The classical as well as the modern treatments of foliar venation in the angiosperms exhibit a common defect, viz.: the failure to consider the entire system of veins and veinlets within the lamina. In VON ETTINGHAUSEN's (1861) treatise, for example, the patterns of the minor venation are not fully exploited and the proposed classification is based primarily upon the course of the major veins. This one-sided treatment of venation is clearly not justified either morphologically or from an anatomical-physiological viewpoint. One of its unfortunate results has been the prevailing assertion in many texts that the leaves of monocotyledons are "parallel-veined"

in contrast to the "net-veined" leaves of dicotyledons. The superficial nature of this supposed difference is shown by the complex reticulum of veinlets (including freely-terminating veinlet endings) found in the leaves of many members of the *Liliaceae*, *Araceae* and *Orchidaceae*. Furthermore, despite the wide use of venation characters in taxonomy, the descriptions and terminologies are very commonly restricted to the obvious features of the venation of unprocessed herbarium specimens. As a consequence, many useful morphological characters have been seriously underestimated or ignored. There is great need therefore for the initiation of both intensive as well as extensive investigations of the complete venation patterns of a wide range of angiospermous genera and families. At the descriptive-morphological level, such investigations should utilize the technique of clearing by NaOH and staining with safranin the entire vascular system of the lamina. But surveys should also be accompanied by (1) a thorough comparison of venation patterns of the cotyledons, juvenile and adult foliage leaves, cataphylls and floral organs (2) and histogenetic study of the venation.

The intricate and largely unexplored nature of foliar venation is strikingly illustrated by the author's study on the four genera of the *Quinaceae* (cf. Amer. Jour. Bot. Vol. 37, No. 2, 1950). The intercostal venation of *Quina acutangula* DUCKE consists of a complex series of plumose veins interconnected by extensive anastomoses, with narrow areoles and infrequent veinlet endings. In contrast, the intercostal venation of *Touroulia* and *Froesia* is formed by an exceptionally regular, closely-spaced arcuate system of branched and anastomosed veinlets. The venation of *Lacunaria*, although less regular, is also of this type. In both *Q. acutangula* and *Touroulia*, successively larger seedling leaves exhibit a progressive development of the venation patterns typical of the adult foliage. The ontogenetic and phylogenetic implications of this transition are briefly discussed.

Discussion

K. ESAU: Complimenting Dr. FOSTER on his beautiful preparations. Also a question: Whether the "line of interference" or "line of union" of minor veins in *Touroulia* and certain other genera is actually a result of ontogenetic union. Since Dr. FOSTER thinks it might be so, it is possible that the peculiar pattern results from a combination of differentiation of procambium with an expansion growth of the lamina.

A. S. FOSTER: In response to Dr. ESAU's question regarding the presumed fusion of the arcuate veinlets in *Iamaulia*, there has yet been no possibility of making exact developmental studies. This raises the question of the direction of differentiation of the protoxylem and protophloem in the veinlets—an important problem for future research.

P. R. BELL (London)

Stelar Structure in the Genus Elaphoglossum

A number of species of *Elaphoglossum* from Jamaica have been examined morphologically. Species having horizontal creeping rhizome and bearing fronds in two alternating marginal ranks possessed a dorsiventral stele, consisting of a large ventral and a small dorsal meristele. Root traces arose solely from the ventral meristele. The two meristeles were joined by marginal bridges and from this bridge and from the margins of the meristeles arose the leaf and bud traces.

Other species, in which the rhizome was not creeping, but obliquely ascendent, and in which the fronds were borne in several ranks on the upper surface, showed a more complex stelar structure. The general pattern of the stele remained the same, but the ventral meristele appeared to have contracted and extra leaf traces to have been intercalated into the dorsal region.

One species in which the rhizome was up right or obliquely ascendent and in which the fronds were not confined to any one side of the rhizome, was found to possess a radially symmetrical dictyostele.

Parallel to this series of stelar forms, another series was discovered showing progressive reduction in the degree of development of the bud trace.

Discussion

R. E. HOLTUM: The record of a species with erect rhizome having radial symmetry in *Elaphoglossum* is interesting, as it has not been reported previously, though in other groups of ferns both dorsiventral and erect rhizomes occur. I consider in all cases the dorsiventral form to be more primitive, and Mr. BELL's demonstration of the transition of structure in the developing lateral stem-bud of *E. vittorum* confirms this. I suggest that experimental stimulation of such lateral buds would provide useful further evidence.

Further contributions to the discussion were given by P. R. BELL and C. W. WARDLAW.

A. MONOYER (Liège)

Contribution à l'anatomie vasculaire de Ceratophyllum demersum L.

L'auteur montre que, malgré l'extrême dégradation du système vasculaire due à la vie aquatique, on peut retrouver des indications suffisantes pour établir le type vasculaire de *Ceratophyllum demersum*.

Ce type comporte deux traces foliaires par segments, chaque faisceau parcourant une hauteur de deux entre-nœuds.

Ce type est comparable à celui qui existe dans le genre *Potamogeton*, ce qui confirme les liens de parenté existant entre ces deux genres: l'un dicotylé, l'autre monocotylé, que d'autres auteurs ont mis en évidence par d'autres voies: embryologie et sero-diagnostic.

SESSION 10 A

July 20th, 9 a. m. — noon

Chairman: F. MARKGRAF, Recorders: F. FAGERLIND and M. RYBERG

SUBJECT:

Various Papers

A. J. EAMES (Ithaca, N.Y.)

Are the Ephedrales Derivatives of Cordaite Stock?

Ephedra is distinct in fundamental characters from *Gnetum* and *Welwitschia*, and constitutes an independent order, the *Ephedrales*. Morphologically it resembles the *Cordaiteles* more than other gymnosperms. Support for this treatment comes chiefly from the morphology and anatomy of cones, nodes and leaves. The staminate and ovulate cones are strictly homologous throughout. The microsporangia are borne terminally on a pair of flattened appendages, which, when fused, form the so-called "column." The ovule is borne terminally on a similar, but greatly reduced appendage, and not on a lateral axis as commonly described. Leaf trace number and stomatal type resemble those of the *Coniferales* and the *Cordaiteles* rather than those of *Gnetum* and *Welwitschia*. The *Ephedrales* and the *Coniferales* perhaps represent parallel lines derived from ancient cordaite stock.

Discussion

J. T. BUCHHOLZ: I find nothing to disagree with in Prof. EAMES's general thesis. Here is only one detail, shown in his diagrams of conifer cone groupings. He shows ovules as strictly terminal, when they stand at the end of a spike or raceme. In my experience such terminal ovules in *Podocarpus* are always bracted, therefore not strictly terminal. In *Taxus* they are not bracted and are truly terminal.

With respect to the relationship of *Ephedra* to Conifers I would place them closer (than

ZIMMERMANN for example) on account of the similarity of embryogeny. All *Ephedrales* have cleavage polyembryony, very similar to that of most Conifers.

W. ZIMMERMANN: Die Auffassung, dass die Sporangienstände von *Ephedra* und *Cordaianthus* homolog sind, hat Herr EAMES überzeugend dargelegt. Wir dürfen aber wohl nicht übersehen, dass die wirklichen Ahnen meist weiter zurückliegen. Daher scheint es mir auch hier wahrscheinlicher, dass die gemeinsamen (und noch unbekannten) Ahnen weiter zurückliegen als die bis heute bekannten Cordaiten.

A. J. EAMES: In my opinion the *Coniferales* and *Ephedrales* represent independent lines of reductions and specialization from Cordaite stock.

Further contribution to the debate was given by J. T. BUCHHOLZ, A. J. EAMES, F. MARKGRAF and W. ZIMMERMANN.

H. PRAT (Montreal)

Manifestation de gradients au cours de la différenciation des tissus végétaux

La notion de gradient est depuis longtemps d'usage courant dans les sciences physiques. Elle a été appliquée à l'étude des organismes animaux par de nombreux embryologistes, notamment BOVERI et CHILD (CHILD, C. M.: Patterns and problems of development 1941). En ce qui concerne les végétaux beaucoup de données ont été recueillies sur diverses catégories de gradients. (PRAT, H.: Les gradients histo-physiologiques et l'organogenèse végétale. Rev. Canad. Biol., 4: 543-693, 1945. Contrib.

Inst. Bot. Univ. de Montréal, 58: 1-151, 1945.
 PRAT, H.: Histo-physiological gradients and plant organogenesis. Bot. Review. 14: 603-643, 1948.) Nous pouvons distinguer parmi ceux-ci en premier lieu des gradients physico-chimiques, tels que des gradients de pH, de rH, de concentration en une substance déterminée: un sucre, un alcaloïde, un acide aminé etc. En second lieu nous pouvons observer des gradients physiologiques, concernant chacun une fonction donnée: par exemple gradient d'intensité respiratoire, de photosynthèse, d'activité mitotique. En troisième lieu peuvent être reconnus des gradients de nature histologique: variations dans la dimension, la nature, la forme des cellules, la proportion de tel type d'élément cellulaire parmi les autres etc. Ces trois catégories de gradients sont en perpétuelle interaction dans l'organisme végétal en cours de croissance. Les Algues les plus simples ne présentent que des gradients intracellulaires. Chez diverses Rhéophycées, par contre, on peut saisir l'apparition de gradients histologiques sous leurs formes élémentaires: Par exemple dans le thalle de *Dichyoneurum*, un gradient transversal multinodal apparaît, révélé par les nervures; il détermine, à partir d'un certain stade, une fenestration de la fronde. Chez *Macrocystis*, un gradient analogue provoque d'abord une fenestration puis une laciniation du sommet du thalle. Chez certaines Rhodophycées, p. ex. *Asparagopsis*, on peut percevoir l'articulation de gradients histologiques élémentaires (cellules photosynthétiques — cellules collectrices) avec les gradients intracellulaires des grandes cellules axiales. Ces exemples montrent comment un système de gradients histo-physiologiques coordonnés peut s'établir dans l'organisme d'une Algue, annonçant l'établissement des gradients beaucoup plus complexes des végétaux supérieurs.

Discussion

F. M. SCOTT: Has the temperature toleration of hydrophytes (phanerogams) and brown algae (*Laminaria* etc) been compared? Anat-

omy differs, but temperature conditions in water are comparatively uniform.

M. CHADEFAUD: Il y aurait intérêt à étendre de telles recherches au cas des Algues siphonnées, qui présentent une grande complexité morphologique, bien qu'elles ne soient pas cloisonnées au cellules séparées.

G. NOACHOVITCH: Dans quelle mesure a-t-on étudié les gradients de lignification des tissus dans les tiges de monocotylédones, et dans celles des Graminées et des Palmiers, en particulier? De tels gradients sont particulièrement remarquables dans le cas de la Canne à sucre, d'une part, et dans celui des *Calamus* d'autre part. La «moëlle» (des praticiens) y est très faiblement lignifiée, d'une manière générale, cette lignification pouvant se limiter aux gros vaisseaux et à quelques cellules et fibres ligneuses des nervures. A la périphérie, au contraire, le parenchyme fondamental est très fortement lignifié, et dans chaque nervure, le liber excepté, presque tous les éléments sont lignifiés, et fortement lignifiés. Entre ces deux types extrêmes s'observe un gradient de lignification, variable avec l'espèce, le génotype, en cause, dont l'étude peut se faire aisément par le moyen de la phloroglucine chlorohydrate, l'intensité de la coloration rouge cerise ou rose obtenue révélant le degré de lignification des éléments histologiques étudiés.

Des études de cette nature présentent un grand intérêt non seulement du point de vue de la physiologie, de la systématique et de la génétique, mais du point de vue économique, d'une manière non moins évidente.

Further contribution to the debate was given by H. PRAT and C. W. WARDLAW.

P. GREUSS (Szeged)
Xylotomie der Koniferen

Zwecks grösserer Übersichtlichkeit werden die Koniferen-Gattungen auf Grund ihrer xylotomischen Eigenschaften in die Gruppen I-

VI eingeteilt, innerhalb welcher noch kleinere Einheiten aufgestellt werden. Als Unterscheidungsmerkmale dienen: Im Querschnitt, ob die Tracheiden eckig oder rundlich sind, ob Harzgänge vorhanden sind, ferner die Schärfe oder Verschwommenheit der Jahresringgrenze, im Tangentialschnitt Höhe und Breite der Markstrahlen, Glätte und Tüpfelung der Tangentialwände der Markstrahlzellen, Tüpfelung und Verdickung der Tracheiden, Glätte und Tüpfelung der Horizontalwände der Parenchymzellen, Stärke und Anzahl der Epithelzellen in den Harzgängen, im Radialschnitt Anzahl, Anordnung und spirale Verdickung der Hoftüpfel auf den Wänden der Tracheiden, Anwesenheit von Markstrahltracheiden, Zusammensetzung der Markstrahlzellen, Tüpfelung der Horizontal-, Tangential- und Radialwände, Vorhandensein von Ansätzen, ferner Anzahl und Beschaffenheit der in einem Kreuzungsfelde befindlichen Tüpfel.

Unter Beachtung dieser Unterscheidungsmerkmale gehören in:

Gruppe I die Hölzer, bei welchen die Tüpfel auf den Radialwänden der Tracheiden in 2-5 Reihen und abwechselnd nicht nebeneinander angeordnet sind, somit die Höfe der Hoftüpfel den Bienenzellen ähnlich sechseckig sind. (*Agathis*, *Araucaria*.)

Gruppe II: Hier bestehen auf sämtlichen Tracheiden einzeln, paarweise, zu viert oder dichter verlaufende relativ dünne spirale Verdickungen erscheinen. (*Amentotaxus*, *Cephalotaxus*, *Torreya*, *Taxus*.)

Gruppe III: Hier bestehen die Markstrahlen aus zwei Elementen, nämlich aus Parenchymen und Quertracheiden. (*Cedrus*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*.)

Gruppe IV: Die Markstrahlen sind homogen, sie enthalten demnach nur Parenchymzellen, deren sämtliche Wände, also die Horizontal-, Tangential- und Radialwände mehrere einfache, zumeist piceoide, cupressoide, juniperoide oder taxodioide Tüpfel aufweisen. Die Tangentialwände sind im allgemeinen perl- oder kammartig verdickt, ausnahmsweise glatt. (*Abies*, *Arceuthos*, *Cupressus*, *Di-*

selma, *Fitzroya*, *Juniperus*, *Keteleeria*, *Libocedrus*, *Pherosphaera*.)

Gruppe V: Hier sind die Horizontalwände der Markstrahlen spärlich oder stark getüpfelt, die Tangentialwände gewöhnlich glatt, höchstens mit 1-2 punkartigen Verdickungen. (*Arthrotaxis*, *Biota*, *Chamaecyparis*, *Cunninghamia*, *Cryptomeria*, *Glyptostrobus*, *Metasequoia*, *Podocarpus*, *Saxegothaea*, *Sequoia*, *Taxodium*, *Thuja*, *Thujopsis*.)

Gruppe VI: Umfasst die Gattungen, bei welchen alle drei Wände der Markstrahlen, also sowohl die Horizontal-, wie auch die Tangential- und Radialwände glatt und dünn sind, höchstens mit primärer Tüpfelung. (*Acropyle*, *Actinostrobus*, *Austrotaxus*, *Callitris*, *Callitropsis*, *Dacrydium*, *Fokienia*, *Ginkgo*, *Metasequoia*, *Microcachrys*, *Phyllocladus*, *Podocarpus*, *Prumnopitys*, *Sciadopitys*, *Taiwania*, *Tetrclinis*, *Widdringtonia*.)

P. CHAMPAGNAT (Strasbourg)

Fixation des préséances sur les rameaux d'un an des végétaux ligneux

Sur une pousse herbacée les bourgeons axillaires sont constamment soumis à l'influence inhibitrice du sommet en croissance. Cette inhibition est hormonale et se poursuit continuellement pendant que dure la croissance.

On admet aussi qu'il existe une interaction de même nature entre les divers bourgeons d'un rameau ligneux d'un an: les pousses à développement faible seraient inhibées par celles qui s'allongent de façon plus intense.

Je vais montrer dans un cas favorable (observations faites sur *Syringa vulgaris* L.) que cette inhibition actuelle n'existe pas chez les végétaux ligneux.

1° — Il y a une correspondance étroite entre les dimensions finales d'une pousse et celles du bourgeon dormant qui lui a donné naissance.

2° — Cette même règle reste valable si, avant l'hiver, on réussit à inverser expérimentalement la position des gros et des petits

bourgeons sur le rameau. (Petits bourgeons au sommet, bourgeons plus gros situés plus bas.) La position réciproque des bourgeons n'influence donc pas leur développement final.

3° — Dans le cas de rameaux sur lesquels 2 paires de bourgeons seulement se développent en pousses longues, l'ablation de la paire la plus vigoureuse, ou son isolement à l'aide d'entailles, ne modifie pas le développement de la paire plus faible qu'elle soit située au dessus ou au dessous.

4° — Dans le cas de rameaux plus vigoureux on note souvent une modification mais elle se produit toujours avec un retard trop considérable (3 à 4 semaines) pour qu'on puisse l'attribuer à la suppression d'une action inhibitrice actuelle.

5° — En faisant varier l'importance des entailles et leur position on montre enfin que c'est l'affluence de substances ascendantes (nutritives?) et non l'influence des autres rameaux qui agit sur le développement de ces jeunes pousses.

Conclusion. Les corrélations entre les bourgeons sur les rameaux ligneux du Lilas sont déjà fixées au moment de la reprise de la végétation du printemps. Cette fixation s'est établie l'été précédent, sur le rameau herbacé, pendant les mois qui ont suivi la fin de la croissance en longueur. Elle règle le gonflement des bourgeons et par suite leur dévelop-

pement au cours de la saison suivante. Le mécanisme des corrélations entre bourgeons permet donc d'opposer nettement pousses herbacées et rameaux ligneux: il y a inhibition par un bourgeon dominant sur les premières; fixation des préséances sur les seconds.

Discussion

P. CHOUARD: La diversité des conditions d'établissement des préséances fixées faisant suite aux corrélations actuelles pourrait être interprétée, à mon avis, en fonction des types de passage des rameaux et des bourgeons à l'état de dormance, p. ex., passage obligatoire et rapide chez le Lilas, passage progressif et moins obligatoire chez le Sureau ou le Robnier.

P. CHAMPAGNAT: Je suis personnellement convaincu de l'importance de la dormance pour la fixation des préséances. Dans de nombreuses espèces basitones par exemple les bourgeons de base entrent en dormance bien avant que d'allongement du rameau ait cessé. Les bourgeons se trouvant près de ce sommet en croissance sont toujours soumis à l'influence hormonale et sont retardés dans leur développement. Ceux de la base, au contraire, peuvent pendant ce temps acquérir un avantage qu'ils conserveront au printemps suivant.

Further contribution to the debate was given by P. CHAMPAGNAT and R. GAUTHERET.

SESSION 10B

July 20th, 9 a. m. — noon

Chairman: F. MARKGRAF, Records: F. FAGERLIND and M. RYBERG

SUBJECT:

Phyllotaxis in Phanerogams

L. PLANTEFOL (Paris)

Les méthodes et les résultats de l'étude phyllotaxique

Parce que la tige feuillée est constituée d'unités qui se répètent, le problème phyllotaxique présente une importance considérable en morphologie. Les méthodes pour le ré-

soudre sont multiples: Etude de la disposition réalisée sur les tiges adultes, normales ou tératologiques. — Etude 1) morphologique, 2) histologique et 3) cytologique de la tige au point végétatif. — Expérimentation sur les points végétatifs. — Toutes ces méthodes imposent l'analyse minutieuse des objets réels, non la considération de schémas idéalisés.

Les résultats d'une telle recherche sont d'abord la dénégation de toute valeur à la théorie classique de la spirale génératrice fondée sur la divergence constante de points foliaires successifs. Un seul des systèmes de lignes (spirale fondamentale, orthostiques et parastiques) du trace classique correspond à une réalité phyllotaxique qu'il s'agit de reconnaître. Presque toujours chez les Dicotylédones, souvent chez les Monocotylédones, la réalité phyllotaxique comporte plus d'une hélice foliaire. Le long de chacune de ces hélices, les feuilles successives sont, par leurs segments foliaires, en contiguité (juxtaposition, chevauchement, superposition). Tous les types de dispositions foliaires normales, spiralées ou verticillées, toutes les prétendues anomalies adaptatives comme celles que constituent par exemple les plantes cactéoïdes, s'interprètent aisément comme les expressions multiples d'une loi unique. L'expérimentation apporte sa confirmation: les résultats classiques désormais de M. et R. SNOW sur la croissance, après une section longitudinale limitée, d'un sommet de tige à feuilles opposées décuissées, montrent la dissociation expérimentale des deux hélices foliaires portées par la tige ou la suppression expérimentale d'une des deux hélices foliaires. Les anomalies rencontrées dans la nature, de la simple dissociation de tige aux fasciations rubannées, s'expliquent par une anormale élévation, très souvent analysable, du nombre des hélices foliaires.

Dans le point végétatif, on ne constate pas le fonctionnement d'initiales superficielles suivant l'axe de la tige. Dans la croissance active des Dicotylédones, les initiales sont distantes du sommet; elles constituent un anneau initial qui fournit les sousassements et initiums des feuilles et se relie au plan des cellules initiales de la partie centrale de la tige. Si les mêmes zones de l'anneau initial demeurent centres générateurs de feuilles, les hélices foliaires sont redressées en orthostiques, avec superposition des ébauches successives. La progression de l'activité méristématique intense depuis une zone de l'anneau initial qui

vient de réaliser un primordium ou un initium, à la zone voisine où va être réalisé un initium foliaire nouveau, amène la progression hélicoïdale de ces hélices foliaires sur la tige adulte, avec juxtaposition des ébauches successives le long d'une même hélice.

F. J. RICHARDS (Harpenden, Herts.)

Phyllotaxis Patterns in Relation to the Growth of the Apex

Current methods of defining the phyllotaxis patterns found at plant apices are both incomplete and ambiguous, largely owing to their neglect of radial primordial spacing. The ratio of the distances of consecutive primordia from the centre of the system, as seen in transverse section, yields a "phyllotaxis index" that, taken in conjunction with the divergence angle, defines completely the primordial arrangement in that plane. The scale of phyllotaxis indices has been adjusted so that in FIBONACCI patterns an integral number indicates orthogonal intersection of a particular FIBONACCI pair of parastichies:

Orthogonal FIBONACCI system ..	1:2	2:3	3:5	5:8	8:13
Phyllotaxis index	1.0	2.0	3.0	4.0	5.0

The calculated index need not be integral, hence phyllotaxis, as actually measured, becomes a continuous function. When the divergence approximates some ideal angle other than the FIBONACCI angle, the phyllotaxis indices of the successive orthogonal systems again increase by steps of unity, but the numbers themselves are fractional, each ideal angle having its own characteristic fractional ending at the various orthogonal parastichy intersections. A slight modification in the calculation enables indices, quantitatively comparable with those described above, to be derived from whorled arrangements, for example the opposite decussate; these may then be quantitatively assessed both relative to one another and relative to apices displaying any other phyllotaxis system whatsoever.

Measurement on a longitudinal section of the angle of inclination towards one another

of opposite sides of the apex in the region where primordia are initiated, provides another number which, when deducted from the phyllotaxis index, yields an "equivalent phyllotaxis index"; if this latter be interpreted, as regards the curve systems, in the same manner as the phyllotaxis index, it reveals the parastichy relations existing on the actual apical surface in the region of initiation. Every equivalent phyllotaxis index corresponds to a particular ratio of two areas: (1) transverse area of the central apical region which produces no primordia, and (2) the actual apical surface area allotted to a single primordium at initiation; both these may be estimated.

Phyllotaxis index may be expressed also entirely in dynamic terms i.e. as a function of (1) apical transverse relative growth rate; (2) rate of change in transverse size of the bare central region at corresponding stages in successive plastochrones; and (3) rate of production of primordia. When (2) is small, the apical transverse growth rate may be estimated from the phyllotaxis index and the plastochrone.

F. FAGERLIND (Stockholm)

The Phyllotaxy and the Fundamental Structure of the Higher Cormophytes

The structure of the more stable sectorial chimaeras shows that the shoots of the higher

Cormophytes represent compositions of parallel and equivalent shoot sectors, originating from separate primordia in the growing apex of the stem. In plants with opposite or whorled leaves, the sectors run perpendicularly. In plants with alternate leaves the course is not always strictly perpendicular but steeply spiral, due supposedly to the presence of torsion processes. Opposite or whorled leaves arise from the simultaneous formation of leaf primordia in the meristematic part of the various sectors. Alternate leaves are due to the fact that the formation of leaf primordia takes place in succession in the different sectors. In some cases each leaf is formed by one primordium deriving from one single sector. In other instances, two or several closely situated sectors together give rise to a leaf. The course of the primary bundles suggests the whole composition. The phyllotactic fractions are explained from the mechanical principles that manifest themselves when a sector-shaped primordium is divided.

Discussion

In the discussion that followed after PLANTEFOL's, RICHARDS's and FAGERLIND's communications, contributions were given by L. PLANTEFOL and W. ZIMMERMANN.



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Vice-Recorder: G. LINDBERG

SESSION 1

July 12th, 1—4 p.m.

Chairman: J. RAMSBOTTOM, Recorder: N. FRIES

SUBJECT:

Significance of Vitamins and Allied Substances to Fungi

W. H. SCHOPFER (Bern)

Les équilibres vitaminiques chez les microorganismes

Une cellule vivante possède un équipement de vitamines qui, normalement, doivent se trouver entre elles dans un état d'équilibre quantitatif. On se rend compte de l'importance de cet équilibre en le troublant, a) en paralysant la biosynthèse d'une vitamine, b) en « déplaçant » une vitamine par son antagoniste spécifique.

a) *Action de la vitamine K₃ (2-méthyl-1,4-naphtoquinone) sur Phycomyces blakesleeianus, (auxo-hétérotrophe pour la vitamine B₁)*

La vitamine K₃ détermine une inhibition du développement; celle-ci est due à une diminution marquée de la biosynthèse de l'acide nicotinique. L'inhibition peut être annulée par l'acide nicotinique ou l'un de ses précurseurs (ac. 3-oxyanthranilique, cynurénine, tryptophane, indol, ac. anthranilique). La perturbation doit donc s'effectuer à un stade précoce de la biosynthèse de la vitamine PP, par un blocage de la synthèse de l'acide anthranilique.

Le métabolisme des autres vitamines est troublé également. On relève une hypervitami-

nose relativement à la riboflavine, l'acide pantothénique, la biotine et, plus faiblement, à la pyridoxine, ainsi qu'une hypovitaminose à l'égard de l'acide nicotinique, de l'acide folique et de la choline. Un excès de vitamine K₃, agissant sur la synthèse de l'acide nicotinique, détruit l'équilibre indispensable à un développement normal.

Cultures pures de racine (Pisum) (avec M. BEIN). Des essais parallèles ont été effectués avec les méristèmes radiculaires. Un déséquilibre, différent en ce qui concerne les vitamines touchées, se manifeste également sous l'influence de la vitamine K₃. Il se produit en particulier une forte hypervitaminose relativement à la pyridoxine (+ 450 %).

b) *Action d'un antagoniste de vitamine. Action de la néopyrithiamine sur Neurospora crassa « thiaminless ».* L'inhibition du développement est accompagnée d'une hypervitaminose relativement à la biotine (+117 %), à la pyridoxine (+75 %), à la riboflavine, à l'acide pantothénique et à l'acide nicotinique, ainsi qu'une hypovitaminose à l'égard de l'acide folique. La destruction de la thiamine ajoutée est fortement accélérée. Ainsi, en touchant à une vitamine par son antivitamine spécifique, on dé-

règle tout le métabolisme vitaminique de l'organisme.

Cultures pures de racine (Pisum) (avec M. BEIN). La néopyrithiamine exerce une forte action inhibitrice, accompagnée des phénomènes suivants: hypervitaminose relativement à la pyridoxine (+ 75 %), à la vitamine B₁₂, à l'acide nicotinique, à l'acide pantothénique, ainsi qu'une hypovitaminose au sujet de la riboflavine. Les taux de biotine restent inchangés.

Ces faits attestent l'importance de la notion d'équilibre vitaminique, insuffisamment prise en considération jusqu'à maintenant, chez les microorganismes et les plantes supérieures. Ils nécessitent une étude approfondie, pour l'instant à ses débuts, du mécanisme de ces interrelations vitaminiques.

F.G. FISCHER und G.WERNER (Würzburg) *Eine Analyse des Chemotropismus bei einigen Saprolegniaceen*

Trotz der Untersuchungen von W. PFEFFER und seiner Schule und solcher aus späterer Zeit waren bisher keine auf Pilzhypphen chemotropisch wirkende, chemisch definierte Stoffe bekannt.

Ausgehend von der chemotropischen Wirksamkeit von Fliegenleichen (J. WORTMANN, 1887), Pollen verschiedener Pflanzen (H. BURGEFF und I. SCHNEEBAUER, 1945), wurde von uns bald die *allgemeine* Verbreitung derart wirkender Stoffe in natürlichem Material erkannt. Als Vorbedingung für ihre Identifizierung wurde ein auf der Krümmung von Hypphen der *Saprolegnia ferax* Thureti (in Agar-Kulturen mit 0,2 Proz. Malzextrakt) beruhender quantitativer Test ausgearbeitet. Die zu prüfende Stofflösung diffundiert aus einem Agar-Säulchen in die Agar-Schicht der Kultur hinein und kann so in genau zu bestimmendem Umkreis ihre Wirkung entfalten.

Osmotische Einflüsse und solche der Aciditätsänderung sind ohne chemotropische Wirkung. Verschiedene Pilznährstoffe und alle bisher bekannten, wasserlöslichen Vitamine und Wuchsstoffe erweisen sich als unwirksam. *Ei-*

weiss-Hydrolysate rufen hingegen noch in hoher Verdünnung starke chemotropische Reaktionen hervor. Doch erzeugen die meisten Aminosäuren *einzel*n geprüft keine Hyphenkrümmung; nur Leucin, Cystein und Glutaminsäure zeigen bestimmte Wirkungen, die sich jedoch von jenen natürlicher Extrakte unterscheiden. *Gemische* von Aminosäuren sind dagegen wirksam. Ein aus reinen Aminosäuren kombiniertes Gemisch z. B., das gleiche Zusammensetzung hat wie ein Casein-Hydrolysat, gleicht ihm auch in der chemotropischen Wirkung. *Die Wirksamkeit organischer Materialien und Extrakte ist auf ihren Gehalt an verschiedenen Aminosäuren zurückzuführen.* 0,001 Gamma Aminosäuren-Gemisch sind mit dem angewandten Test noch gut nachweisbar.

Durch Auswertung verschiedener Aminosäure-Kombinationen wird die relative Beteiligung bestimmter Aminosäuren an der chemotropischen Wirkung geprüft. Eine Unentbehrlichkeit bestimmter Aminosäuren konnte nicht festgestellt werden. Das Erscheinungsbild der chemotropischen Reaktion (Hyphenkrümmung und gerichtetes Hervorsprossen von Seitenhypphen) zeigt bestimmte Abhängigkeiten von der qualitativen Zusammensetzung der Aminosäure-Kombination. Die Stärke der Wirksamkeit der Kombinationen ist nicht ihrem Stickstoff-Gehalt proportional. Mindest-Kombinationen von 5-7 Aminosäuren aus den verschiedenen Gruppen, z. B. Leucin + Methionin + Phenylalanin + Lysin + Glutaminsäure, sind erforderlich, um das Bild des Chemotropismus durch Eiweiss-Hydrolysate nachzuahmen.

Das Zustandekommen der Hyphenkrümmung zum Diffusionszentrum hin muss bewirkt werden durch Unterschiede in der Aminosäure-Konzentration zwischen gegenüberliegenden Seiten der wachsenden Hypphenspitze; auf der Seite der höheren Konzentration ist das Längenzustand geringer. Unter den angewendeten Bedingungen reagiert die Hyphe schätzungsweise noch auf Konzentrationsunterschiede von Casein-Hydrolysat zwischen entgegengesetzten Flanken von ca. 0,00001 Gamma/mm³.

Die Wirkung chemotropischer Vorgänge auf die Wuchsform des Pilzmycels und die ökologische Bedeutung des positiven Chemotropismus werden in einigen Versuchen geprüft.

Die Hervorlockung der Antheridien von *Achlya polyandra* durch die Oogonien und ihre Hinleitung zu diesen, wird höchstwahrscheinlich ebenfalls durch Eiweissabbauprodukte hervorgerufen. Es liessen sich jedenfalls auf Oogonien zuwachsende Antheridien dieses Pilzes in Agar-Kultur in Richtung eines mit Casein-Hydrolysat versetzten Agar-Klumpchens ablenken.

Es bleibt zu prüfen, ob Aminosäuren-Gemische auch bei anderen Pilzfamilien und -ordnungen Chemotropismen hervorrufen.

Der Vortrag wurde von G. WERNER gehalten.

Discussion

G. A. DE VRIES: There was to be seen a difference in the place of the side branches on the bending hypha when comparing the last series of photos and the first series. In the first series the origin was very abundant on the side turned to the agar block with the diffusing substance, in the last series the branching took place more on the outer side. Is there any explanation for this difference?

G. WERNER: In der zuerst gezeigten Serie liegen die sich krümmenden Hyphen *innerhalb* des Mycels, in der anderen Serie am *Rande* des Pilzmycels. Aus dem unbewachsenen Malz-Agar (Malz enthält selbst Aminosäuren und ist deshalb chemotropisch wirksam) fliesst daher ein Diffusionsstrom von Aminosäuren in Richtung zum bewachsenen Agar, da innerhalb dessen die Aminosäuren grösstenteils assimiliert sind, und erzeugt an den bereits gekrümmten Hyphen Aussprossungen in Richtung auf den unbewachsenen Agar und nicht zum Agarblock hin. Das Diffusionsgefälle des vom Agarblock ausgehenden Diffusionsstromes von Aminosäuren ist an dieser Stelle bereits so abgeflacht (sechs Stunden nach Aufsetzen des Agarblocks) und deshalb unwirksam.

Z. G. BÁNHIDI: Zeigt sich etwa ein Unter-

schied zwischen mit Säure (HCl) oder Trypsin hydrolysiertem Kasein hinsichtlich seiner chemotropischen Wirksamkeit? Wie bekannt ist nämlich nur im Säure-Hydrolysat Tryptophan zerstört; es sind also die auf beiden Wegen hergestellten Kasein-Hydrolysate in ihrer Aminosäuren-Zusammensetzung nicht identisch.

G. WERNER: Ein „synthetisches“ Kasein-Hydrolysat ohne Tryptophan-Zugabe lässt, verglichen mit tryptisch verdaulichem Kasein, keinen wesentlichen Unterschied in der chemotropischen Wirkung erkennen.

J. MAGROU, H. MARNEFFE, et F. MARIAT (Paris)

Action morphogène des vitamines sur certains champignons

Sphaerocybe concentrica Magrou et Marneffe, 1945¹ est un champignon de la famille des Stilbaccées caractérisé par ses fructifications corémiées disposées en cercles concentriques et formées par un stipe fibreux, brun, rigide, constitué par des faisceaux d'hyphes enroulés en spirale, et portant une tête fructifère subglobuleuse, d'abord jaune vif, puis virant au vert et produisant des conidies hyalines, lisses, ovoïdes ou globuleuses, acropleurogènes, solitaires ou en courtes chaînes, s'insérant sur de fins stérigmates. Ce champignon ne produit ses corémies caractéristiques qu'en présence d'aneurine; en l'absence de cette vitamine, il développe un mycélium stérile. Dans une première série d'essais, nous avons obtenu aussi des corémies en présence de thiazole, mais l'expérience, répétée avec un nouvel échantillon de ce produit, ne nous a plus donné le même résultat; la culture de *Phycomyces Blakesleeanus* en présence de notre premier échantillon y a révélé la présence d'aneurine en quantité notable, et c'est à cette impureté, et non au thiazole lui-même, qu'il convient d'attribuer la formation des corémies. Mais le thiazole pur, associé à la pyrimidine, permet la fructification; le champignon est donc capable d'opérer la synthèse de l'aneurine aux dépens des deux fractions de cette vita-

¹ Bull. Soc. Mycol. de France, 61, 5 (1945).

mine. On peut encore provoquer la fructification dans un milieu renfermant de la pyrimidine mais dépourvu d'aneurine ou de thiazole, à condition d'associer un champignon producteur de thiazole (*Rhodotorula rubra*), à *Sphaerocybe*, qui se trouve ainsi en mesure de synthétiser l'aneurine nécessaire à la production de ses corémies: celles-ci se développent le long de la ligne de contact entre les deux colonies associées. L'un de nous¹ a obtenu la formation des périthèces d'une Sphériaciée (*Sordaria fimicola*), qui ne fructifie qu'en présence de certains facteurs de croissance, sur un milieu exempt de vitamines où avait été ensemencé *Sphaerocybe concentrica*, qui fournit les facteurs nécessaires au *Sordaria* et fructifie lui-même sous l'action des vitamines élaborées par la Sphériaciée.

La concentration minima d'aneurine permettant la formation de corémies bien différenciées de *Sphaerocybe* est 4×10^{-9} .

Deux conclusions se dégagent de ces diverses constatations: Elles visent: 1°) l'action morphogène que les vitamines exercent sur certains champignons, — 2°) le rôle éventuel joué, dans les associations symbiotiques, par les vitamines que les deux partenaires peuvent mutuellement se fournir.²

Discussion

W. H. SCHOPFER:

1. L'action de la vitamine B₃ est-elle quantitative ou une dose limite agit-elle d'une manière définitive?

2. Le thiazol de 1944 agissait; celui de 1950 n'est plus actif. Les auteurs admettent que le thiazol de 1944 est contaminé par de l'aneurine. Ne peut-on pas admettre une évolution ayant transformé le champignon à thiazol en organisme à pyrimidine + thiazol?

3. La culture mixte *Rhodotorula rubra* + *Sphaerocybe* se fait en présence de pyrimidine. Il s'agit donc d'une stimulation unilatérale et non pas d'une symbiose (stimulation bilatérale).

¹ MARIAT, F.—C. R. Acad. Sciences, 228, 68 (1949).

² MAGROU, J., MARNEFFE, H., & MARIAT, F.—Ann. Inst. Pasteur, 80, 443 (1951).

F. MARIAT:

1. Une dose limite agit de façon définitive. Aux concentrations de 3×10^{-9} et au-dessous les corémies manquent; à la concentration de 4×10^{-9} et au-dessus elles se produisent en abondance. La concentration de 4×10^{-9} d'aneurine marque donc le seuil d'activité de la vitamine.

2. L'hypothèse d'une telle évolution est très probable. Elle se trouve d'ailleurs appuyée par le fait que la morphologie de notre champignon s'est modifiée au cours de ces dernières années.

3. Il s'agit en effet d'une stimulation unilatérale, toutefois, M. MAGROU estime que le terme de symbiose n'est pas impropre.

A. A. BITANCOURT and VICTORIA ROSSETTI (São Paulo)

The Role of Thiamin in the Nutrition of *Phytophthora* spp.

In a previous paper we have shown that thiamin, an indispensable growth substance for the *Phytophthora* spp., the causal agents of footrot of *Citrus*, does not affect the growth in diameter of the thallus on agar medium. It increases the ramification of the hyphae, thus thickening the thallus, which can be conveniently measured by the amount of light transmitted through it, as measured with a photocell.

The growth in diameter is increased when, to an otherwise complete synthetic medium solidified with a special agar, are added extracts of plant material, such as potato broth or substances diffused from plant tissues, such as disks of *Citrus* bark placed on the surface of the medium during 4 hours, before inoculation.

To account for this effect we have surmised the presence in the plant material of a factor, "L", responsible for the elongation of the main hyphae of the thallus. Factor L is also contained in the common agar (*Gelidium*) but not in the special brand of agar mentioned above.

In further studies with *Phytophthora citrophthora* we have found that under reduced pressure (20 mm of Hg) the ramifications do not

develop, whether the medium contains thiamin or not. To interpret this result we assume that a third factor, "R", is involved. Factor L and thiamin are not synthesized by the fungus and must be added to the medium. Factor R is normally produced by the fungus but its effect is inhibited at low oxygen pressure. At pressures below 20 mm the inhibition of the effect of factor L also occurs and the fungus does not grow.

It would seem that thiamin does not directly induce the ramification of the mycelium as concluded from our previous studies, but controls some condition prior to it, such as the division of the nuclei.

Discussion

A. QUISPEL: You have assumed a factor R to explain the absence of ramifications under reduced pressure. Might it be possible that this effect is merely caused by the change from an aerobic to an anaerobic metabolism? Or have you any reasons to assume a specific factor?

A. A. BITANCOURT: The postulation of factor R is a useful working hypothesis. The term "factor" in this instance should be taken in its broadest sense. Undoubtedly the reduced pressure induces a change from an aerobic to a partially anaerobic metabolism. We postulate that the growth of secondary hyphae is the result of a peculiar metabolic activity involving a system of substrates and enzymes normally produced by the fungus. This system requires oxygen at a higher pressure than the systems responsible for elongation of the main hyphae and the inception of ramification. Factor R may therefore be taken as the first mentioned system, or better as that part of the system which ensures the metabolism in which oxygen is used.

GRACE M. WATERHOUSE asked whether depth of agar had been considered and what was the depth used, as this factor has a considerable effect on the hyphal branching in *Phytophthora* spp.

A. A. BITANCOURT: In standard Petri dishes,

for instance, we use 25 ml of medium, which gives a uniform depth of 7 mm. In many cases treatments and check were contained in the same dish. Thus any factors which might affect hyphal branching equally affect treatments and checks. In all experiments the significance of treatment differences was established by statistical analysis of the results.

N. FRIES (Uppsala)

Intermediates in the Biosynthesis of Purines in Fungi

Unlike many bacteria, all fungi so far investigated are capable of synthesizing their essential purines themselves. A favourable effect of an addition of adenine is, however, often obtained in pure culture experiments. Although this might indicate a somewhat insufficient synthesizing power, other interpretations must also be considered, particularly because of the interactions demonstrated between adenine and certain indole-derivatives.

With the aid of artificially produced biochemical mutations a certain insight can be obtained into the biosynthesis of purines in fungi. In my particular test-organism, the Ascomycete *Ophiostoma multiannulatum*, as well as in the better known fungus *Neurospora crassa*, two different types of adenine-less mutants have been found, one capable of utilizing adenine or hypoxanthine, the other, more rare, requiring adenine and not being capable of using hypoxanthine. The former is termed, hypoxanthine-less, the latter, adenine-less. In *Ophiostoma*, there are also found guanine-less mutants, which require guanine, but cannot utilize adenine or hypoxanthine.

Since SHIVE and coworkers have claimed (1947) that an imidazole compound, 4-amino-5-carboxamide-imidazole, is a precursor of purines in bacteria, I have tested the effect of this substance on the purine-deficient mutants mentioned. This investigation was carried out in collaboration with BERGSTRÖM and ROTTENBERG at the University of Lund. Some of the

hypoxanthine-less mutants proved to be the only ones capable of utilizing the 4-amino-5-carboxamide-imidazole. A few other imidazole-compounds of a more simple constitution were completely or almost completely inactive in all cases tested. These facts support the assumption that the biosynthesis of adenine starts with the formation of the particular imidazole-compound mentioned, and then proceeds via hypoxanthine as an intermediate.

The sparing action produced by guanine in the hypoxanthine-less and adenine-less mutants indicates that in *Ophiostoma* guanine is formed from adenine (and/or hypoxanthine?). How this transformation takes place, is not yet clear. It appears, however, that the guanine-less mutants are capable of utilizing 2,6-diamino-

purine as well as guanine, but not xanthine or isoguanine, which makes it at least possible that 2,6-diamino-purine is an intermediate in this transformation.

There are many facts indicating that the substances involved in these transformations are not the free bases but rather their nucleosides or nucleotides.

The guanine-less mutants are obviously rather rare, and the very few ones hitherto isolated seem to represent the same biochemical type. However, a method has now been worked out in *Ophiostoma*, permitting a selective isolation of guanine-less mutants. It is thus possible that new biochemical types can be found, throwing more light upon the question of the formation of guanine.

SESSION 2

Jointly with Section TCR: July 14th, 9 a. m. — noon

Chairman: J. RAMSBOTTOM, Recorders: J. A. NANNFELDT and N. FRIES

SUBJECT:

Phylogeny and Systematics of Ascomycetes

L. E. WEHMEYER (Ann Arbor, Mich.)
Considerations of Some Methods of Approach to the Taxonomic Study of the Fungi

The taxonomy of a group such as the Ascomycetes is regarded as having a dual aspect, the actual variable population, as it exists in nature, and the man made arrangement which attempts to reflect this situation and at the same time act as an artificial index system.

It is an inherent quality of the human mind that it must work with separately integrated entities, which in this case are the categories of our systematics. Nature, on the other hand, does not always present such entities. Much of the confusion in the Ascomycetes is due to the fragmentary and uncorrelated erection of a large number of such overlapping entities.

The ideal, natural system should first determine the actual plan of the natural plan

before any species are delimited. In nature, this population arises by the production, segregation and recombination of a large number of minute unit characters, resulting in a mass of overlapping variant individuals. Such evolution may occur at different points on the earth's surface at different rates, or in a somewhat different manner, resulting in geographic or ecologic groups. As evolution proceeds some of these character groupings will disappear for one reason or another, resulting in isolated species or groups comprising higher categories. There will remain, however, large populations consisting of a continuous series of overlapping variants. These individuals make up our more complex species groups, or larger genera. This hypothetical situation is what would be expected if the mechanics of Mendelian heredity apply to the fungi. It is also the situation actually found in those groups of the asco-

mycetes which have been most intensively studied (i.e. *Fusarium*, *Aspergillus*, *Penicillium* etc.).

This general plan of variation can be determined in any group only by the study of a large enough series of individuals, from a wide geographical range, to give a representative cross section of its evolutionary trends. Once this plan is determined, the second purpose of our taxonomic scheme, the erection of the man made index, may be undertaken. It should be recognized that a species is a man made concept, that does not always exist in nature, and allows a certain flexibility, and must often be somewhat arbitrary as long as species are delimited upon a correlated basis and reflect the plan already detected.

Since we conceive of a species as a genetic entity, we may rule out environmental and fluctuating variations so far as they may be determined. There remain four bases used for species separation in the Ascomycetes: 1—morphologic variation; 2—physiologic variation; 3—host limitation; 4—life history differences. The increasing demands of both plant and human pathology and industrial application in the Ascomycetes demand that we recognize increasingly fine differentiations in all four of these categories. In fact we are approaching the limit of individual variation and if we give specific names to all such variations we will soon be so naming every collection or isolation. For this reason, the speaker is strongly of the conservative opinion that species ranks should be limited to morphologic variation, for these are most easily determined by the average worker without special apparatus or technique.

The needs of the specialist must also be met, but can be taken care of by the use of sub-specific categories (variety, form, race). Such usage does not force the average mycologist to struggle with an overburdening number of names which can be determined only by special means, but at the same time provides a machinery whereby the finer distinctions of a fungus entity can be made available to those needing them. Furthermore, sub-species ranks indicates the relationships between such minor varieties,

whereas such relationships are not obvious when specific names are used for each sub-group. These same principles apply in a general way to the higher categories.

Our standard, usable taxonomic arrangement should be kept conservative, even though somewhat artificial. Fragmentary and hypothetical arrangements are of value to our advance, but should not be inserted in the general scheme, until most details have been worked out upon the principles mentioned.

Discussion

O. JAAG: Die vom Referenten diskutierten Probleme gelten in derselben Bedeutung in der Algologie. Die Abklärung der entwicklungs-geschichtlichen morphologischen und physiologischen Eigentümlichkeiten, so weit als dies möglich ist, soll die Grundlage bilden für die Beschreibung und Umgrenzung von Arten und kleineren systematischen Einheiten. Nur auf Grund dieser Kenntnis wird es möglich sein, ein natürliches System von Pilzen und Algen aufzubauen.

I. REICHERT: I wish to draw the attention of the audience to the danger of basing mycology and using it in nomenclatural practice on the ascoferous stage and discarding the names of the conidial stage. We shall then obtain a wrong picture of the distribution as the ascoferous stage only occurs under certain climatic conditions. Take, for instance, *Venturia*. This ascoferous stage is not to be found in arid areas and the fungus, as far as it does occur (in mountains, or in the winter), is propagated by the conidial stage only. I therefore suggest not to use for the practice the ascoferous names but the conidial ones.

MARCELLE LE GAL (Paris)

Revision de la position taxonomique du genre Trichophaea Boudier et ses conséquences du point de vue phylogénétique

BOUDIER crée les genres: *Trichophaea*, *Cheilymenia*, *Melastiza*, *Anthracobia*, *Pseudombro-*

phila, qu'il classe auprès des *Ciliaria* QUÉL. (Bull. Sté. Myc. Fr. I, 105, 1885.) Mais les auteurs continuent de réunir toutes ces espèces, avec les *Lachnea* FR. sensu BOUD., dans un genre unique appelé successivement: *Lachnea* FR. emend., *Scutellinia* KUNTZE, *Patella* WEBER, *Lachnea* GILLET.

Chez les *Trichophaea*, les caractères sont plus primitifs: spores parfois asymétriques, lisses ou formations ornementales du type le plus simple ou réticulation édifiée en deça de l'assise sous-périsporique et non calloso-pectique comme chez les *Phillipsia*; thèques à parois épaisses, avec hernies latérales comme chez les *Cookeina*, à déhiscence suboperculée (anneau apical ouvert). Espèces sans pigments de carotène; poils d'origine superficielle.

Chez les *Ciliaria* QUÉL., les caractères sont plus évolués: spores symétriques, ornées, parfois à formations ornementales du type le plus complexe; thèques à déhiscence operculée (entonnoir à tractus). Paraphyses à filaments de carotène, mais poils à crampons en liaison avec la couche moyenne filamenteuse de la chair donc d'origine profonde comme chez *Cookeina* *Tricholoma* (MONT.) KUNTZE.

Mais *Trichophaea Erinaceus* (SWEIN.) nov. comb. a des poils, de même type, indiquant une parenté d'origine avec les *Ciliaria*.

Les *Melastiza*, voisins des *Ciliaria*, sont encore plus évolués: ornements sporaux toujours de formation complexe, poils d'origine superficielle.

Chez les *Lachnea* sensu BOUD.: spores lisses ou ornements de type simple; thèques à déhiscence operculée. Espèces plus grandes, plus cupulées; pas de filaments de carotène; poils superficiels moins raides, aspect de feutrage comme chez la tribu des *Urnulae* (*Sarcoscyphaceae*).

Mais *Trichophaea atro-fusca* (REBENT.) BOUD. est nettement cupulé. Ses poils sont de deux types: raides comme ceux des *Trichophaea*, onduleux comme ceux des *Lachnea*. Donc le genre *Lachnea* sensu Boud. a peut-être une origine commune avec les *Trichophaea*?

Pseudombrophila Romagnesii LE GAL (Rev. Myc., 2, 219, 1937) possède une déhiscence sub-

operculée et des poils en faisceaux comme chez les *Cookeina*.

Ces caractères différentiels paraissent justifier les coupures génériques de Boudier, notamment le genre *Trichophaea*.

Mais à la base des *Humariacées* BOUD. existent encore d'autres groupes à déhiscence suboperculée, notamment les *Psilopezia* BERK. et les *Phaedropezia* LA GAL, nov. gen.

Tous ces groupes différents des *Sarcoscyphaceae*, aussi suboperculés, essentiellement par leur consistance charnue, jamais élastique, subéreuse ou gélatineuse. Leurs thèques sont plus courtes, moins flexueuses.

Ils sont affines aux Operculés, tandis que les *Sarcoscyphaceae* sont affines aux Inoperculés (*Giboriacées* BOUD.) par les *Plectania*, dont plusieurs espèces exotiques minuscules ont la consistance et l'allure de certains *Rutstroemia*.

Discussion

J. A. NANNFELDT: BOUDIER's distinguishing of *Operculates* and *Inoperculates* has now won an admirable continuation in the working out through Dr. LE GAL of the *Suboperculates*.

K. CEJP (Praha)

Proposals for Characterizing the Taxonomic Units of Fungi Imperfecti

The so-called *Fungi imperfecti* FÜCKEL (*Deuteromycetes* SACCARDO, CLEMENTS and SHEAR, *Adelomycetes* LANGERON) do not quite fit into the framework of the unified system of endings for the correct designation of the rank of the taxonomic units as proposed and formed by L. CROIZAT (1945), V. JIRÁSEK (1945) for phanerogams and cryptogams, as they do not form a natural but only an artificial group taxonomically, and include fungi of which we usually know only the conidial stages. Most botanical authors in their textbooks consider them as a separate class of fungi, and only relatively few mycologists place them as a mere appendix to the class *Ascomycetes* (*Ascomycetinea* CEJP and JIRÁSEK 1945) or as an appendix of the class *Fungi*.

The classification of the group *Deuteromycetes* was and is up till now according to the conidiophors in three groups which most authors call orders giving them also the usual ending -ales. They are the *Phomales* (*Sphaeropsidales*, *Sphaeropsidaceae*, etc.), *Melanconiales* and *Hyphomycetales* (*Hyphomycetes*, *Hyphales*, etc.). Still lower units were then formed by the families with the ending -aceae (e.g. *Melanconiaceae*, *Dematiaceae*, etc.), which are further divided into subordinate groups, to which ENGLER (1919), for instance, gives the ending -eae (e.g. *Micronemeae*, etc.), often in connection with the word spora (e.g. *Dictyosporae*, etc.).

As the *Deuteromycetes* are a purely artificial group, it is not possible in their classification to use the systematic units with their corresponding endings established for plant groups phylogenetically related. We propose therefore for the classification of the appendix of the fungi, the *Deuteromycetes*, five new classification units in the following descending order: cumulus, subcumulus, pseudofamilia, cohorts, subcohors. For the cumuli, i.e. the three main groups referred to above, the ending -mycetes can be used; this ending is to the point and does not occur anywhere in this sense among the new proposals for a unification of the higher taxonomic units (see V. JIRÁSEK in *Věda přírodní*, vol. 13, No. 6: 165-167, Prague 1945). As the linguistic basis for the designation cumulus we can use with advantage a designation of the morphological character of the mycelium (e.g. stroma) or of the conidiophors. Thus we get three cumuli: *Pycnomycetes* (= *Phomales*), *Stromatmycetes* (= *Melanconiales*) and *Hyphomycetes*. Instead of the former families ending in -aceae I propose the term pseudofamilies (with the ending -atae), e.g. *Phomatae*, etc.; and as lower units cohorts (with the ending -spora) and subcohors (ending in -formes). The designations of these part units can be found easily from the name of the principal representative or also of the type of the group in question to which the appropriate ending is added.

Instead of the designation genus it is cer-

tainly more appropriate to use in the group *Deuteromycetes* the designation pseudogenus (cf. Formgattung, form-genus, "genus," D. P. LIMBER 1940, D. P. ROGERS 1948) and instead of species the designation pseudospecies (cf. Nebenart); perhaps they will become before long current members of the nomenclatoric alphabet.

A brief survey of the classification of the appendix *Deuteromycetes* of the phylum *Mycophyta* would according to our proposal be as follows (we designate the cumuli A, B, etc.; the pseudofamilies 1, 2, etc.; the cohorts a, b, etc.; the subcohors α , β , etc.):

- A. *Pycnomycetes*, 1. *Phomatae*, a. *Hyalosporae*, b. *Phaeosporae*, $\alphaConiothiriformes etc. 2. *Zythiatae*, etc., 3. *Leptostromatae*, etc., 4. *Discellatae*, etc.$
- B. *Stromatmycetes*, 1. *Melanconiatae*, a. *Hyalosporae*, $\alphaColletotrichiformes etc.$
- C. *Hyphomycetes*, 1. *Moniliatae* etc., 2. *Dematiatae* etc., 3. *Tuberculariatae* etc., 4. *Stilbatae* etc.

A. MUNK (Silkeborg, Denmark)

Some Remarks on Relations between Stromatic and Non-Stromatic Pyrenomycetes

In the literature on *Pyrenomycetes*, the word "stroma" is commonly used for macroscopically well differentiated parts of the mycelium, containing, or at least to be found in coherence with, the perithecia. A priori, this conception does not seem to have any great morphological value; and a comparative study of the *Pyrenomycetes* has shown me that the presence or absence of a "stroma" is a character of a most inferior morphological and phylogenetical importance. This conclusion will be illustrated by examples, both from ascohymenial groups (*Xylariaceae*, *Diaporthaceae*) and ascolocular groups (different taxonomic units within *Pseudosphaeriales*). In connection with this negative conclusion emendations of families will be proposed on the basis of other characters occurring in mutual correlation. Further, a new family within *Pseudosphaeriales*, *Herpotrichiellaceae* n.

fam., will be proposed and discussed. It represents a good example of the negative value of the character stromatic/non-stromatic; one of its genera (*Berlesiiella* SACC.) has been placed in *Cucurbitariaceae*, whereas species of other genera have been placed in *Melanomma* FCKL., in separate genera (*Herpotrichiella* PETR., *Capronia* SACC.), or have not been discovered before, i.e. new genera will have to be erected.

Discussion

J. A. VON ARX: Meine Untersuchungen mit *Pseudosphaeriales* (= *Dothideales*) zeigten dieselben Ergebnisse wie die MUNKS. Wir dürfen diese Pilze nicht nach Vorhandensein oder Fehlen eines Stromas einteilen, da dieser oft vom Substrat beeinflusst ist und den ungeschlechtlichen Teil des Fruchtkörpers darstellt. In erster Linie muss auf den geschlechtlichen Teil, auf die Fruchtschicht, Rücksicht genommen werden.

Bsp. bei den *Pseudosphaeriales*:

nicht stromatisch:

Guignardia, *Pyreniella*, *Discosphaerina*

Mycosphaerella

Pleospora, *Clathrospora*

Venturia, *Coleroa*

Stigmataea, *Phaeocryptopus*

mit Stroma:

— *Botryosphaeria* (*relanops*)

Cymadothea

Cucurbitaria, *Fenestella*

Lasiobotrys

Gibbera, *Atopospora*

L. E. WEHMEYER: I quite agree with Mr. MUNK that the distinction of stromatic and non-stromatic forms is an artificial one which cuts across natural lines of development. "Stroma" has probably developed in a different way in several different lines of development.

This is an illustration of the conflict between the older traditional conservative classification and our newer concepts of phylogenetic relationships. The question is "whether" or "when" to introduce these new concepts into

our older schemes. The difficulty is that the new concepts are always incomplete and if inserted in a conservative arrangement, have a large number of species and genera which do not fit into the newer concepts.

A. MUNK: Dr. WEHMEYER is right; the new classification can hardly be worked together with the conservative system. I never meant to do so. But, contrarily to Dr. WEHMEYER, I do not think it is premature to construct a new natural classification.

A. J. MIX (Lawrence, Kans.)

Studies in the Genus Taphrina. Behavior of Various Species as to Utilization of Nitrogen Compounds

Following recent studies (MIX, 1949) in which species of *Taphrina* were distinguished by morphology of the ascus-state, investigation has been made of the ability of twenty-eight species and fifty-six host-forms to utilize various nitrogen compounds. Since ROBERTS (1946) has suggested a possible relationship between *Torulopsis pulcherrima* and *Taphrina deformans*, thirteen species of *Torulopsis* were also studied.

A liquid medium of KH_2PO_4 2.75 g, $\text{MgSO}_4 \cdot 7 \text{H}_2\text{O}$ 1.25 g, dextrose 10.0 g, distilled water 1000 ml was used. To this different nitrogen compounds were added to furnish the nitrogen-equivalent of two grams KNO_3 per liter. Each solution was prepared with and without thiamine hydrochloride, one part per million.

Though rate of growth was studied only utilization or refusal of substances will be reported here. Peptone, urea, eight ammonium compounds, five nitrates, and twenty amino acids or related compounds were used.

Summary of results

1. All species and forms of *Taphrina* refused ammonium acetate.

2. Twelve species showed different patterns of nitrogen utilization: *T. aesculi*, *T. americana*, *T. californica*, *T. farlowii*, *T. johansonii*, *T.*

nana, *T. polystichi*, *T. populina*, *T. pruni-subcordatae*, *T. thomasi*, *T. tosquinetii*, *T. virginica*.

3. Three species from *Acer* behaved differently toward inorganic nitrogen compounds. Further, *T. dearnessii* used fourteen amino acids; *T. letifera* used twelve of these and two more; *T. sacchari* used the same fourteen as *T. dearnessii* and two more.

4. a) Certain host-forms agreed with each other in behavior: *T. carnea* from *Betula intermedia* and from *B. lutea*; *T. deformans* from *Prunus communis* and from *P. persica*; *T. flavorubra* from *Prunus pumila* var. *susquehanae* and *P. besseyi*; *T. populi-salicis* from *Populus fremontii* and from *P. trichocarpa*; *T. sadebeckii* from *Alnus glutinosa* and from *A. rugosa*; *T. ulmi* from *Ulmus alata* and from *U. fulva*.

b) *T. epiphylla* and the summer form described as *T. klebahnii* behaved alike.

5. a) Some host-forms showed differences. *T. communis* from fruits of *Prunus americana*, from twigs of the same host (formerly *T. decipiens*), from fruits of *P. lanata* and of *P. nigra* agreed in their behavior.

b) *T. communis* from fruits of *Prunus angustifolia* (*T. mirabilis* var. *tortilis*) from twigs of *P. angustifolia* (*T. mirabilis*) and of *P. maritima* differed from the preceding by utilizing one additional amino acid.

c) *T. confusa* from *Prunus virginiana* and from *P. virginiana* var. *demissa* differed in that the former refused two amino acids, the latter refused these two and five others.

d) *T. cerasi* from *Prunus avium* used fifteen amino acids; the form from *P. pennsylvanica* all twenty.

e) *T. betulina* from *Betula pubescens*; from *B. intermedia* (*T. lapponica*), and from *B. pendula* (*T. turgida*). The first named (only) refused NH_4Cl and used all amino acids, the second used twelve amino acids; the third the same twelve and one more.

6. The twelve host-forms of *Taphrina caerulea* behaved like separate species. The form from *Quercus coccinea* used all compounds but three amino acids. By contrast the form from *Q. prinoides* made slight use of inorganic com-

pounds except NH_4NO_3 ; used twelve amino acids.

7. All thirteen species of *Torulopsis* used ammonium acetate. Nine species used all nitrogen compounds. *T. dattila*, *T. kefyr*, and *T. pulcherrima* were highly selective.

Literature

ROBERTS, C. A comparative study of *Torulopsis pulcherrima* and *Taphrina deformans* in culture. — *Farlowia* 2: 345-383 (1946).

MIX, A. J. A monograph of the genus *Taphrina*. — *Univ. Kansas Sci. Bull.* 33: 1: 3-167 (1949).

Discussion

W. P. K. FINDLAY asked whether the speaker had found any differences in behaviour towards different sources of nitrogen between different isolations of *Taphrina* sp. from the same host.

A. J. MIX: Differences were found between different isolates but not to the degree found between species and host-forms.

V. SCARDOVI (Bologna)

Some Remarks on the Life-Cycle of *Torulopsidoideae*

It is to day generally admitted that sporeforming yeasts are phylogenetically strictly related to *Ascomycetes* on the basis of their sexual reproduction; they have been grouped, according to the modern classifications, into the ascomycetous family of *Endomycetaceae*. If phylogenetic relationships between sporogenous yeasts and *Ascomycetes* have been so cleared up, not the same is true concerning the non-spore-forming yeasts, whose systematic position is to day surrounded by great uncertainty, mainly because of the paucity of stable taxonomical characters. In 1925 KLUYVER and VAN NIEL considered as strictly related to *Basidiomycetes* a salmon-colored, non-spore-forming yeast belonging to the genus *Sporobolomyces*, on the basis of a particular discharge mechanism of stalk-provided kidney-shaped cells formed at the colony surface, this mechanism being shared only

by higher *Basidiomycetes*. From these and from NADSON and PHILIPPOV's early observations upon mutational phenomena induced by X-rays in a *Rhodotorula*-like yeast strain, the idea has emerged (see HENRICI's monograph of 1941) that the entire group of ordinary rose-colored yeasts should be related to *Basidiomycetes*. No general agreement exists as to the validity of this assumption, whose fallacy is due either to the absence of cytological characters of basidium and basidiospores, according to LOHWAG, GUILLIERMOND and CIFERRI, or else to the fact, pointed out by STEMPELL, that this particular discharge mechanism is shared by fungi other than *Basidiomycetes* (*Taphrina* etc.). Assuming that only cytological characters can probably throw some light on this intriguing question, and the data available on the cytology of non-spore forming yeasts (*Torulopsidoideae*) being today very scanty, a strain of *Torulopsis*, characterized, like a few representatives of this genus, by the power of synthesizing an amylose-like substance in acidic media, has been submitted to a first series of cytological investigations. In passing it may be mentioned that the same amylose-like substance is produced by a strain of *Bullera* (Derx) received from the Delft Laboratory, a fungus which is said to be related to *Basidiomycetes* as well as *Sporobolomyces*. Having previously ascertained that in media at pH values as 4 or 5 the so-called "giant cells" are very rapidly and abundantly formed, formation process and subsequent development of these cells has been firstly examined by growing several normal cells in moist chamber under the microscope. A rather extensive photomicrographic documentation, which for lack of space cannot be reported here, has been collected at each step of the process. Fusion of two adjacent normal cells has been found to be the prerequisite for these cells being formed; plasmogamy is then

normally followed by caryogamy, so that "giant cells," at the nuclear staining, may appear both uni- and binucleate. Single nucleus divides subsequently into four nuclei when these cells are transferred into fresh neutral medium. These four nuclei migrate at the subsequent stage either through germination tube into a large and elongated body, or directly into four stalk-provided cells outgrown from the "giant cell" itself. Circumstantial evidence is available as to the further migration of the nuclei into four stalk-provided cells, which are formed at the distal part of the elongated body mentioned. Dycaryotic cells have been consistently found, but their origin is difficult to be traced with certainty. Cytological data reported witness to the complexity, not so far supposed, of the life-cycle of these non-spore-forming yeasts and if we suppose—a supposition which seems to be not completely unwarranted—that fusing cells are aploid, we are entitled to say that the observed process seizes our imagination by its recalling the fundamentally similar process of the "holobasidium" formation. Though we are well aware that it is dangerous to attach a too far-reaching significance to these first results and to interfere uncautiously about relationships between this yeast and *Basidiomycetes*, we feel sure that this and future work, performed along these lines, will provide a hint toward the solution of this interesting problem.

Literature

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SESSION 3

Jointly with Section TCR: July 14th, 1—4 p. m.

Chairmen: J. RAMSBOTTOM and C. W. EMMONS, Recorders: J. A. NANNFELDT and N. FRIES

SUBJECT:

Phylogeny and Systematics of Basidiomycetes

R. HEIM (Paris)

Esquisse sur la phylogénie des Basidiomycètes

Parmi les Basidiomycètes, des critères d'affinité, que peu à peu les mycologues ont tirés de la physionomie, de la morphologie, de l'anatomie, de l'embryologie, de la biochimie, de la génétique, ont révélé successivement leur insuffisance en tant qu'indices exclusifs ou absolus. Ainsi, des notions classiquement fondamentales sont apparues fausses.

Selon leur origine, la valeur de certains dispositifs ou caractères très manifestes varie. L'anneau de nature pseudoangiocarpique ne saurait suffire à séparer les uns des autres quelques Bolets, ou Russules, ni les *Termitomyces*. Le *Clitocybe tabescens* exannulé est génériquement inséparable de l'*Armillariella mellea*. Le bourrelet des *Tricholomes* annelés (*T. fovealis*) est sans valeur générique. La coloration de la spore peut ne revêtir qu'une signification inconstante: Lépiotes (dont la gamme de teinte sporale varie du blanc au pourpre et à l'olivâtre foncé).

Les notions d'Agaricacés, Gastéromycètes, Hypogés, comme celles d'Ustilaginales, d'Hétérobasiidiés, sont artificielles.

Les Agaricales ne sont nullement caractérisées par des lamelles: les *Agarics* à hyménium poré (*Dictyoplaça*, *Poromycena*, *Phaeomycena*, *Mycenoporella*, *Mycomedusa*) sont des Mycénés parmi lesquels le tube acquiert progressivement son individualité; des genres à hyménium lisse sont rattachables aux Agaricales (certaines *Cyphelles* aux *Pleurotes*, *Skepperia* et *Cymatella* aux *Marasmes*).

Dans les Porohydnés se placent des champignons lamellés: *Lenzites*, certains *Lentinus* et *Panus*, les *Schizophyllum*.

Les Chanterelles sont intimement liées à des Clavaires.

Les Bolets ne sont pas toujours tubulés: Paxilles, Phyllopores et *Xerocomus* sont inséparables, les *Gyrodon* proches des Polypores; les *Strobilomyces*, gastéroïdes, sont loin des *Ixechnus* subnigricoles, à tubes indépendants (eux-mêmes bien distincts des *Fistulines* à rapprocher des *Solenia*), de même que des *Phlebopus*, à sclérote et pied subexcentrique.

Les Hypogés réunissent des formes de convergence, beaucoup résultant de la dégradation progressive d'Hyménomycètes épigés: les *Hydnangium*, *Arcangiella* sont des Astérosporaux équivalents à des formes souterraines et simplifiées de Lactario-Russulés, les Rhizopogons de Bolets, le *Richoniella* des Rhodophylles.

Des Gastéromycètes dérivent de Champignons devenus peu à peu angiocarpes, formes dégradées d'Hyménomycètes: entre les *Martellia* hypogés et les Russules annelées on trouve les *Macowanites* et les *Elasmomyces*; entre Rhizopogons et Bolets le g. *Dodgea*; entre *Secotium* et Conocybes le g. *Galeropsis*; entre *Gyrophragmium* et Coprins le g. *Montagnies*, etc. Les caractères de symétrie, de dimensions, de silhouette sporales, la position du pore germinatif, sont inconstants parmi ces formes de transition.

Les Phalloïdées marquent le stade d'évolution ultime de l'un des phylums dont le groupement taxonomique constitue les Holobasidiomycètes.

R. SINGER (Tucumán)

Antibiotic Activity and Formation of Ectotrophic Mycorrhiza in Relation to Natural Affinity in the Classification of the Basidiomycetes

On the basis of the author's own experimental work as well as that carried out by LAVIANO with the author's collaboration, and the numerous tests made by others, especially WILKINS, ROBBINS, and some European and Australian investigators, the genera and species tested for antibacterial activity were arranged in the order of the SACCARDO classification and then in a parallel list in the order of the author's own¹ classification. As for the first list, it can be stated that no apparent relationship exists between the taxonomic position and the kind of activity observed. In the second list based on—as we think—more natural generic units, it can be shown that there is a relationship between the taxonomic position and the bacteriostatic action of the fungous extracts or the broth. Similar lists were compared for those fungi which form ectotrophic mycorrhiza with forest trees, and the result is essentially the same, even more pronouncedly so since there is much more variation between individual strains in the production of antibiotics than there is in fungus-host relation. While, however, the methods of obtaining the pertinent data in antibiotics research are all due to a single procedure which is essentially experimental and quantitative, the experimental data on ectotrophic mycorrhiza must naturally be supplemented by coordinated, prolonged, and careful observation in the field in different regions of the earth.

Some species of the genus *Tricholoma sensu lato* are found to show a rather consistent action against Gram-negative bacteria. These species are scattered in the genus *sensu lato*. In the natural classification, they belong to the new genus *Tricholomopsis* Sing., or else to a recently emended genus *Lepista* (*Rhodopaxillus*), or else to the most primitive subgenus of *Tricholoma*

with clamp connections, interwoven epicuticular hyphae, intracellular pigment, typified by *Tricholoma saponaceum*. *Collybia platyphylla* was transferred to *Tricholomopsis*, and corresponding to what was to be expected, the activity against Gram-negative bacteria is as distinct and constant as in other species of *Tricholomopsis*. Among the *Flammulas* and *Pholiotas* in the larger sense, we find occasional activity against Gram-positive bacteria but in a natural classification it will be seen that all those with reasonably constant bacteriostatic activity belong to the genus *Gymnopilus*. Even the strangest case—two species of *Agaricus* belonging to two different sections, according to the classification of the author being the only ones of the genus showing activity against Gram-negative bacteria—has been cleared up satisfactorily. Those strains of *Agaricus arvensis* which showed this activity were misdetermined according to Dr. WILKINS and belong to *Agaricus xanthoderma*. Similarly, it seems that all Australian strains showing anti-Gram-negative activity are conspecific with *Agaricus xanthoderma*; consequently all species and strains with positive action belong to the section *Xanthodermei* Sing. On the negative side, it is remarkable that many genera and whole families (the Gomphidiaceae and the Rhodophyllaceae) seem to be completely devoid of antibacterial activity.

As for the mycorrhizal relationship, it must be indicated again that in the *Tricholomas* in the larger sense we find species with obligatory ectotrophic mycorrhiza scattered all over the Friesian sections. In a more natural classification, the split groups *Tricholomopsis* and *Lepista* contain all the species which are non-mycorrhizal, and the subgenus *Tricholoma* containing *Tricholoma saponaceum*, mentioned before, also contains species either non-mycorrhizal or without obligatory mycorrhiza-formation. There is a marked parallelism between the absence of antibacterial action and the presence of mycorrhiza relationships in this group as in several other groups of Basidiomycetes.

¹ SINGER, R. The Agaricales in Modern Taxonomy.—Lilloa 22. 1949 (1951).

In the genus *Boletus* sensu lato, those species which show an exclusive or almost exclusive affinity to coniferous mycorrhizal hosts, are scattered around in the SACCARDO-scheme whereas in the classification proposed by the author, they are combined in a subfamily Suilloideae containing the genera *Suillus* (*Ixocomus*), *Boletinus*, and *Psiloboletinus*. In another genus, *Leccinum* (*Krombholzia*) the species show an exclusive or almost exclusive affinity to mycorrhizal hosts belonging to the orders Salicales and Fagales. In the old conception of the genus *Boletinus*, the most typical conifer species are mixed up with species forming mycorrhiza with *Fraxinus* (viz. *Boletinus porosus*).

Regarding the family Hygrophoraceae, it has been argued that the Fayodian genera composing the old genus *Hygrophorus* sensu lato, are too closely related to be kept apart since the distinguishing characters are nearly all anatomical. Recent mycorrhiza studies and field observations show, however, that obligatory mycorrhizal formation with trees of the Salicales, the Fagales, *Tilia* and the conifers exists only in one of these genera, the genus *Hygrophorus* (*Limacium*).

In the Cortinariaceae, one may say that the best character separating *Gymnopilus* from *Cortinarius* is the growth rate of the mycelium in standard test tube cultures. While the former grow readily and rapidly in the ordinary media under these circumstances, the latter do not. The *Cortinarii* also differ from the *Gymnopili* in being—as far as known—restricted to certain forest trees with which they form ectotrophic mycorrhiza while *Gymnopilus* is saprophytic, or parasitic, or forms endotrophic mycorrhiza with orchids.

If it is true that—as our experience shows—certain genera like *Hygrophorus sensu stricto*, *Tricholoma sensu stricto*, *Catatelasma*, *Amanita*, *Hebeloma*, *Alnicola*, *Cortinarius*, all Gomphidiaceae and most Boletaceae and Russulaceae are strictly mycorrhizal, one would readily conclude that it would be absurd to expect representatives of these groups in floristic lists of regions where trees with which they are obligatorily

linked are completely absent. Such a region is the tropical to subtropical belt of the Selva Tucumano-Boliviana, Argentina and Bolivia. In fact, a thorough survey of the mycoflora of this region shows that no such fungi occur. As soon, however, as the zone of the subalpine Alnetum is reached, or when, further to the south, we enter the zone of *Nothofagus*, the situation is reversed. Both *Alnus jorullensis* and the species of *Nothofagus* form mycorrhiza with Basidiomycetes as could be demonstrated by the author on rootlets. In pure stands of these woods, the same familiar genera forming mycorrhiza with Fagales are collected, e.g. *Cortinarius*, *Russula*, *Lactarius*, *Tricholoma sensu stricto*, *Alnicola*, *Gyrodon*, *Boletus*. The main difference between the mycorrhizal species of the southern and the northern hemisphere is merely a different floristic distribution whereby the number of species in *Lactarius* and *Boletus* is strongly reduced, and *Hygrophorus* is absent in the South.

These examples which could be multiplied with the greatest of ease, prove that the taxonomist finds a better correlation of morphological and biological characters when a modern natural system of classification is used, and that consequently he can guide, to a certain degree, those working in applied fields by helping to plan research on the basis of systematic affinities. He can do this by evaluating the possibilities of a certain group for a given purpose and then determining the chances of a given species within this group by a tentative generalisation.

R. FALCK (Atlanta, Ga.)

Die Degobasidie und die Degobasidiales. Ein Beitrag zum orbisvitalen System

Form, Funktion und Lebenskreis

Unsere orbisvitalen Systematik geht vom Grundsatz aus, dass in der Regel keine Gestaltungen, Funktionen und Eigenschaften der Lebewesen vererbt werden, bevor sie entstanden, ausgebildet und erblich fixiert wurden,

abgesehen von cyto- und somato-symbiontischen Bindungen.¹

Erbliche Organe, Funktionen und Eigenschaften können daher erst durch die Ursachen ihrer Entstehung und erblichen Fixierung wissenschaftlich definiert und essentiell verstanden werden.

Der Neuerwerb von Organen, Funktionen und Eigenschaften und ihre erbliche Fixierung unterscheiden die Lebewesen ebenso grundsätzlich von der leblosen Materie wie ihr phylogenetischer und ontogenetischer Entwicklungsgang.

Als die primären Ursachen jeder neuen Organbildung betrachten wir innere reaktive Dispositionen des Organismus und äussere Faktoren seines umweltlichen Lebenskreises. Ein wesentlicher Faktor der reaktiven Fähigkeiten ist die Entwicklungshöhe, die ein Organismus durch vorangehende Entwicklungsstadien bereits erblich erreicht hat.

Wir wollen hiernach die Systematik und das Verstehen der Organisation nicht allein auf stammesgeschichtliche Merkmale der Vergangenheit und verwandtschaftliche Beziehungen stützen, sondern zugleich auf ihre gegenwärtig in Funktion befindlichen, mit ihren umweltlichen Lebensbedingungen in Reaktion stehenden Organbildungen. Naturgemäss stellen wir hier die letzteren in den Vordergrund.

Acto- und Degobasidie

Im I. Bande der „Grundlinien eines orbisvitalen Systems der Fadenpilze“ wurde dargelegt, dass Neu- und Umbildungen der Organe in progressiver und in retrogressiver Richtung erfolgen.

So kann die Basidie der höheren Fadenpilze aus ihrer energetisch höher entwickelten activen zur niederen inactiven Form retrogressiv zurückgebildet werden und damit ihre Funktionen für die Sporenverbreitung einbüssen.

Sie wird im Gegensatz zur Actobasidie als Degobasidie bezeichnet.²

In jedem Mikrobilde des Hymeniums und jedem Makrobilde der ganzen Frucht ist die Degeneration der Degobasidie leicht erkennbar.

Nach solchem Verlust ist die Degobasidie nicht einmal als „Conidienträger“ anzusprechen, weil sie ihre Sporen nach der Reife nicht mehr tragen, an der Luft bilden und emporheben kann. Zur Zeit der Sporenreife ist sie bereits vergangen.

Die Degobasidie konnte mit demselben Namen wie die Actobasidie bezeichnet werden solange die Abstammung und die Bildungsähnlichkeit als wesentlichste Charaktere für Benennung und Systematik massgebend waren.

Auch die Dego-Basidiospore ist grundlegend verändert, nicht mehr mit kinetischer und potentieller Energie ausgerüstet und zur Verbreitung durch Temperaturströmungen nicht mehr befähigt.³

Sie besitzt aber neue Ausstattungen, besonders durch die ebenfalls umgebildeten Fruchtkörperorgane, die auch nicht mehr der Luftverbreitung der Sporen dienen. Z. B. erschliesst die Vesocarpiumycetenfrucht den Sporen den Weg für ihre Fortentwicklung auf ganz neuen veränderten Verbreitungswegen.²

Wenn also auch eine weitgehende Reduktion der energetischen Charaktere von Sporen und Basidien bei den Degobasidiales eingetreten ist, so ist andererseits ihr biologischer Entwicklungsgang als ein fortgeschrittener zu betrachten. Ausserdem erscheint ihr Synkarion tiefer und vollendeter im Entwicklungsgang verankert, als bei den vorangegangenen Actobasidiales.³

Progression und Retrogression

Die Dego-Abkömmlinge der Phragmobasidiales sind in unsern Listen vorangestellt, in der

¹ The types of symbiotic linkage and their significance for the formation of highly organized forms, functions and lifespans in the phylogenetic process of development. Published by the Research Council of Israel, Jerusalem, 1950. (Simultaneously in the Palestine Journal of Botany, Rehovot Series, Vol. VIII, 1949.)

² Grundlinien eines orbisvitalen Systems der Fadenpilze. I.-II. Teil, H. de Bussy Verlag, Amsterdam, 1948.

³ Grundlinien III. Teil: Der Karyologische Entwicklungsgang und seine Bedeutung im orbisvitalen System der Fadenpilze. Göttingen 1950. Universitäts-Druckerei. Wir verweisen auch auf die begriffliche Trennung der Klassen und Sektionen S. 90-92.

LISTE I

Sektionen und Klassen der Degobasidiales

A. *Dego-Phragmobasidiales* (= *Degostufen der Protobasidiomyceten*)

Stammesgeschichtliche Sektionsordnung	Orbisvitale Klassenordnung	Bisherige Familien- und Gattungsordnung
I. DEGO-AURICULARIALES	a. HAERANGIOMYCETES auricularia-degenes	<i>Hoehnelomycetaceae</i> <i>Hoehnelomyces</i> <i>Stilbum</i>
	b. VENTANGIOMYCETES auricularia-degenes	<i>Phleogenaceae</i> <i>Pilacre</i>
II. DEGO-TREMELLALES	c. HAERANGIOMYCETES tremelladegenes	<i>Sirobasidiaceae</i> <i>Hyaloriaceae</i>
	d. HYDRANGIOMYCETES tremelladegenes	<i>Tulasnellaceae</i>
III. DEGO-PROBASIDIALES	e. CHLAMYDO-VENTANGIO- MYCETES	<i>Ustilagineae</i> von <i>Euustilago</i> bis <i>Proustilago</i>
	f. CHLAMYDO-CONTANGIO-MYCETES tremelladegenes	<i>Tilletiaceae</i>

B. *Holo-Dego-Basidiales* (= *Dego-Stufen der Auto-Basidiomyceten*)

IV. DEGO-AGARICALES	g. VENTO-CARPIO-MYCETES agarico-degenes	<i>Secotiaceae</i> <i>Podaxon</i>
	h. CHLAMYDO-CARPIO-MYCETES agarico-degenes	<i>Hemigaster</i> <i>Nyctalis</i>
V. DEGO-POLYPORALES	i. ZOO-CARPIO-MYCETES polyporo-degenes	<i>Ptychogasteraceae</i> <i>Sclerodermaeae</i>

C. *Holo-Neo-Basidiales* (= *Neo-Stufen der Dego-Auto-Basidiomyceten*)

VI. NEO-CAPILLIALES	m. VENTO-CARPIO-MYCETES capillophores	<i>Podaxon</i> <i>Lycoperdaceae</i>
VII. NEO-PERIDIALES	n. VENTO-CARPIO-MYCETES peridiophores	<i>Tulostomaceae</i> <i>Calostomaceae</i> <i>Geastraceae</i> <i>Sphaerobolaceae</i>
	o. BOLO-CARPIO-MYCETES peridiophores	
	p. PERIDIOLOMYCETES	<i>Nidulariaceae</i>
VIII. NEO-CENTROFUNIALES	q. <i>Vesco-carpio-mycetes</i> centrofuniales	<i>Gauthiera</i>
	r. VESCO-CARPIO-MYCETES centrofuniales	<i>Hysterangium</i>
IX. NEO-LIQUESCOTRAMALES	s. ZOO-CARPIO-MYCETES tramavolvaes	<i>Protuberia</i>
X. NEO-RECEPTACULATES	t. FLORO-CARPIO-MYCETES receptaculates	<i>Clathrus cancellatus</i> <i>Clathrus columnatus</i> <i>Clathrella</i>
XI. NEO-RECEPTACULOPHORES	u. FLORO-CARPIO-MYCETES pediculates	<i>Simblum</i> <i>Colus</i> <i>Kalchbrenneria</i> <i>Lysurus</i>
XII. NEO-SPECTACULOPHORES	v. FLORO-CARPIO-MYCETES spectaculophores	<i>Aseroë</i>

XIII. NEO-PILEOPHORES	w. FLORO-CARPIO-MYCETES pileophores	<i>Phallaceae</i>
XIV. NEO-INDUSIOPHORES	x. FLORO-CARPIO-MYCETES indusiophores	<i>Dictyophora</i>

LISTE 2

Orbisvital System der Degobasidiales mit zugehörigen Sektionen

A. Phragmo-Dego-Basidiales (Proto-)

Orbisvitalen Klassenordnung nach den aktiven Frucht-Organen	Degene Sektions- Ableitung	Familien und Gattungen
I. HAERANGIUM	Dego-phragmo-basidiales	<i>Hoenedomycetaceae</i>
1. HAERANGIOMYCETES	<i>Auriculariaceae</i> Dg. <i>Tremellaceae</i> Dg.	<i>Sirobasidiaceae</i> <i>Hyaloriaceae</i>
II. VENTANGIUM	Phragmo-dego-basidiales	<i>Phleogenaceae</i>
2. VENTANGIOMYCETES	<i>Auriculariaceae</i> Dg.	
III. CHLAMYDO-VENTANGIUM	Phragmo-dego-basidiales	
3. Chlamydo-ventangio- mycetes	<i>Cysto-basidiaceae</i> Dg. <i>Tremellaceae</i> Dg.	<i>Ustilagineae</i> <i>Tilletiaceae</i>

B. Holo-Dego-Basidiales (Hymeno-dego-mycetales)

IV. VENTOCARPUM	Holo-dego-basidiales	
4. Ventocarpiumycetes	<i>Agaricaceae</i> Dg. <i>Capilliphores</i> Ne.	<i>Secotiaceae</i> <i>Podaxon</i> <i>Lycoperdaceae</i> <i>Tulostomaceae</i> <i>Calostomaceae</i> <i>Geastraceae</i>
	Peridiophores Ne.	
V. CHLAMYDOCARPUM	Holo-dego-basidiales	
5. Chlamydo-zoo-carpio- mycetes	<i>Agaricaceae</i> Dg.	<i>Hemigaster</i> <i>Nyctalis</i>
	<i>Polyporaceae</i> Dg.	<i>Ptychogastraceae</i>
VI. ZOO-CHORO-CARPUM	holo-dego-basidiales	
6. Zoo-choro-carpio-mycetes	<i>Agaricaceae</i> Dg. et Ne.	<i>Secotiaceae</i>
7. Zoo-choro-carpio-mycetes	<i>Polyporaceae</i> Dg. et Ne.	<i>Protogaster</i> <i>Melanogastraceae</i> <i>Sclerodermaceae</i>
VII. VESCOCARPUM	Holo-dego-basidiales	
8. Vesco-carpio-mycetes	<i>Tramaglobates</i> Ne.	<i>Rhizopogon</i> <i>Hymenogastraceae</i>
VIII. BOLOCARPUM	Holo-dego-basidiales	
9. Bolocarpio-mycetes	Peridiophores?	<i>Sphaerobolaceae</i>
IX. PERIDIOLOCARPUM (?)	holo-dego-basidiales	
10. Peridiolo-carpio-mycetes	cubiculoglebrates	<i>Nidulariaceae</i>
X. FLOROCARPUM	holo-dego-basidiales	
11. Florocarpio-mycetes	tramavolvates	<i>Protuberia</i>
12. " "	receptaculo-glebrates Ne.	<i>Clathrus</i> <i>Clathrella</i>
13. " "	receptaculo-pediculates Ne.	<i>Sinobium</i> , <i>Colus</i> , <i>Kalchbrennera</i> , <i>Lysurus</i>
14. " "	spectaculophores Nn.	<i>Aseroë</i>
15. " "	Pileophores Nn.	<i>Phallaceae</i>
16. " "	Indusiophores Nn.	<i>Dictyophora</i>

Anm. Dg. = degonascant = rückgebildete Fruchtkörper, Ne. = neonascant = neu gebildete Fruchtkörper, Sporen an Degobasidien gebildet und das Synkarion beherrscht den Entwicklungsgang.

noch unbewiesenen Annahme, dass sie den Holo-basidiales genetisch vorangegangen sind.

Unter den Dego-Phragmobasidiales sind die Ustilaginales die wichtigsten. Ihre unbekannten Urbasidien haben die retrogressiven Umstellungen in ähnlichen Richtungen vollzogen wie die der Dego-Holobasidiales.

Die wichtigsten Unterklassen der Ustilaginales sind die folgenden:

1. Das Chlamydo-Ventangium für die Windverbreitung, z. B. bei dem Formentypus *Ustilago*.
2. Das Chlamydo-Contangium für die Haftverbreitung, z. B. bei den Formen des Typus *Tilletia*.
3. Das Chlamydo-Entomotangium für die Insektenverbreitung, z. B. bei *Ustilago violacea*.
4. Das Chlamydo-Hydrotangium für die Wasserverbreitung, z. B. bei der Gattung *Doasansia*.

Wenn die Urbasidie der Ustilaginales eine Acto-Basidie war, so ist bei ihr die Retrogression noch erheblich weiter fortgeschritten wie bei den von der Holo-Actobasidie abgeleiteten Gasterales.

BREFFELD hat dagegen die Degobasidie der Ustilagineen als eine neue, noch unfertige, der Actobasidie vorangegangene „Hemibasidie“ angesprochen.¹

Ebenso haben erst in jüngerer Zeit SINGER² und andere Autoren, auf die er sich bezieht, auch die Holo-Degobasidiales (Gasterales) als Vorläufer der Actobasidiales zu erweisen versucht, worauf wir hier nicht näher eingehen.

Die verschiedenen stammesgeschichtlichen Systemableitungen selbst bei den Degobasidiales, denen Nachweise ihrer Abstammung nicht fehlen, haben uns zu dem Versuch geführt, die Systematik zugleich auf experimentell erweisbare Merkmale orbisvital zu begründen.

Wir halten aber daran fest, die stammesgeschichtliche Begründung, dort wo sie hinreichend belegbar ist, für unsere orbisvitale Systematik mit auszuwerten. Dafür erbringt diese kurze Mitteilung weitere Unterlagen.

¹ Vergl. von TAVEL, Vergl. Morphol. der Pilze 1892.

² SINGER, R., Das System der Agaricales. Ann. Myc. 34 (1938).

Klassen und Sektionen

Schon der Fortbestand der kernodynamischen Bindung des Synkarions in den inaktiv gewordenen Klassen der Degobasidiales rechtfertigt den Leitsatz, dass diese Charaktere tiefer und langfristiger in der Organisation verankert wurden als die sporenergetischen und die mit ihnen zusammenhängenden organellen Charaktere der Basidiensporen- und Fruchorgane.

Umgekehrt haben die letzteren einen höheren orbisvital biologischen Gegenwartswert.³

Die sporenergetischen und die organellen Charaktere begründen in der orbisvitalen Systematik den Begriff der Klassen, die kernodynamischen Charaktere die einer Mehrzahl von Klassen gemeinsam sind, den Begriff der historischen Verwandtschaftsgruppen, die wir vorläufig als Sektionen bezeichnet haben.⁴

In unserer Liste 1 vereinigen die Sektionen die neuen Klassen zu den natürlichen, stammesgeschichtlichen Sektionsverbänden.

Schlussbetrachtung

Die Grundlage der auf makro- und mikroskopischem Gestaltungsvergleich gestützten Pilzsystematik der älteren Autoren vertreten durch CARL VON LINNÉ (1737), ELIAS MAGNUS FRIES (1837) und CHRISTIANUS HENRICUS PERSOON (1796), die den Artbegriff als einen unveränderlichen betrachteten, konnte durch die Stammbaumsysteme der Genetiker im Zeitalter der Phylogenie nicht grundlegend erschüttert werden; ihre neuen Übergangsformen sind heute noch unstritten.

Durch die umfangreiche cytologische Forschung, deren Methoden das unbekannte Formen- und Entwicklungsreich der Kerne erschlossen haben, konnten die alten Systemgrundlagen erweitert und ergänzt, aber nicht bedeutsam verändert werden.

Ebenso will die orbisvitale Systematik die Gestaltungsgrundlagen mit ihren genetisch-cytologischen Richtungen eher klären als zu ändern versuchen.

Ihre Bedeutung sehen wir darin, den Sinn

³ Aus Grundlinien III Kap. XXIII, 2 letzte Seiten.

⁴ Aus Grundlinien III Kap. XXIV S. 90-92.

und den Lebensinhalt der Formen, Funktionen und Entwicklungsgänge verständlich zu machen und diesen sinnvollen Inhalt als den wissenschaftlichen Kern ihres Artharakters und ihres essentiellen Substanzdaseins zu betrachten, hinausreichend über die axiomatischen Gebundenheiten der unbelebten Materie.

R. KÜHNER (Lyon)

Quelques caractères microscopiques des mycéliums et des germinations d'Agaricales utilisables en systématique

Sommaire de la communication:

Jusqu'à présent les caractères mycéliens des Agarics ont été surtout décrits incidemment à l'occasion de recherches orientées vers la solution de problèmes de sexualité générale ou de spécification. Les travaux effectués par mes élèves et par moi-même à la Faculté des Sciences de Lyon, au cours des six dernières années, conduisent à l'idée que l'étude microscopique du mycélium et des germinations fournit des renseignements qui peuvent faciliter l'appréciation des affinités des espèces et des genres, et qui légitiment, dans une grande mesure la subdivision des Agaricales d'après la couleur des spores.

Chez nombre de leucosporés une spore donnée peut pousser un tube germinatif à chacune de ses extrémités; les exceptions à cette règle s'observent surtout dans les genres *Mycena* et *Marasmius*, où le cytoplasme abandonne progressivement la spore, puis la base du tube germinatif, généralement unique, y jalonnant son retrait de quelques cloisons rapprochées; de telles cloisons de retrait ne s'observent presque jamais chez les chromosporés, bien qu'on ne compte chez eux qu'un tube germinatif par spore.

Le nombre des noyaux dans les articles terminaux des hyphes en croissance est un caractère de grande importance. Dans le mycélium primaire ces articles sont généralement uninucléés comme les autres (et comme souvent les spores elles-mêmes) chez les leucosporés, alors qu'ils renferment souvent plusieurs noyaux chez les chromosporés à spores binucléées.

Lorsque le mycélium secondaire présente un nombre plus ou moins considérable de cloisons sans boucles, les articles terminaux sont en général bi- (ou tri-)nucléés comme les autres chez les leucosporés (*Tricholoma*, *Rhodopaxillus*) et les *Rhodophyllus*. Lorsque, dans un mycélium secondaire à boucles nulles ou rares, les articles terminaux renferment plus de 2 ou 3 noyaux, il ne s'agit en général ni d'un leucosporé, ni d'un *Rhodophyllus*, mais d'un *Pluteus*, *Coprinus*, etc.

Le mycélium primaire produit des oïdies en chaînes droites ou spiralées chez des chromosporés appartenant à des genres les plus variés; il n'est pas rare que leur formation soit accompagnée d'une contraction cytoplasmique. Chez les leucosporés les oïdies n'ont été observées que dans quelques groupes (*Collybia*, particulièrement *Tephrophanae*, et certains *Clitocybe*); les oïdiophores sont moins différenciés, droits, et la contraction est indistincte. Sont dépourvues d'oïdies de très nombreuses espèces de leucosporés (*Mycena*, etc.) et la plupart des Agarics totalement privés de boucles.

Présenté par M. DOUIN.

H. ROMAGNESI (Paris)

Sur les rapports des Cyphellinées avec certains groupes d'Agaricales

Les Cyphellinées, qui réunissent les Basidiomycètes à carpophores cupuliformes ou tubiformes, à hyménium lisse, sont actuellement classées parmi les Aphyllophorales, dans la sous-tribu des Corticiées. Il est certain que les *Cytidia*, les *Porothelium* et même peut-être quelques *Solenia*, y semblent bien en place. Mais quelques observations précises nous ont permis d'entrevoir qu'un assez grand nombre de *Cyphella* et *Solenia* présentent des affinités plus ou moins étroites avec certains groupes d'Agaricales.

Au siècle dernier, DE SEYNES avait été déjà frappé — quoiqu'il n'en ait tiré aucune conclusion d'ordre taxonomique ou phylogénétique — par l'existence d'Agarics cyphelliformes, dont il avait étudié le développement; il cite

en particulier *Pleurotus Craterellus* DUR.-LÉV., que SINGER a récemment classé dans son genre *Chaetocalathus*, et nous pourrions y ajouter *Scytinotopsis cyphelliformis* (BK.) PILÁT et *Kavini* PILÁT, dont la ressemblance morphologique avec les *Cyphella* est réellement remarquable. De plus, certains *Leptoglossum*, dont l'hymenium plissé est précisément à mi-chemin entre l'hymenium lisse des *Cyphella* et lamellé des *Agarics*, ont une forme et un développement cyphelloïdes, qui ont fait envisager à PILÁT un point de contact entre eux et les *Cyphellinées*.

D'ailleurs, quelques *Cyphella* ont aussi un hymenium un peu plissé, par exemple *C. lactea* BRES. et *lactea* FR. SS. PAT.; plusieurs sont longuement stipitées, ou présentent même un carpophore ouvert sur le côté (ou pour le moins nutant), qui constitue une transition avec la silhouette piléolée des petits *Agarics* à stipe grêle (*Delicatula*, etc.); ainsi en est-il des deux espèces citées ci-dessus et de *C. albomarginata* PAT. Enfin, la consistance des espèces du sous-genre *Hydrocyphella* PILÁT et même de nombreux *Glabrotricha* PILÁT d'une part, des *Solenia* grises d'autre part, rappelle soit celle des *Delicatula*, soit celle des *Scytinotopsis*.

Mais ces rapprochements demeurent très vagues et ne sauraient avoir qu'une valeur indicative. Nous nous sommes donc attachés à étudier les caractères microscopiques et microchimiques des quelques espèces que nous avons nous-même récoltées ou que nous avons pu étudier dans les Herbiers du Museum de Paris, et nous avons relevé des analogies si remarquables avec plusieurs familles d'*Agaricales*, que nous ne nous serions guère expliqués comment elles avaient pu passer à peu près inaperçues, si ce n'était un fait bien connu que l'habitat et la taille minuscule de ces plantes ont détourné d'elles l'attention des Agaricologues, pour en faire plutôt l'apanage des spécialistes des *Aphylophorales*.

Notre objet est de signaler ici les plus significatives de ces analogies.

Chez *Cyphella villosa* FR. ex PERS., les poils extérieurs de la cupule, quoiqu'ils soient sur

toute leur longueur finement hérissés de cristaux, rappellent ceux de *Mycena osmundicola* LANGE par leur forme. En outre et surtout, ils sont puissamment métachromatiques, et il suffit d'une infime quantité de Bleu de Crésyl dissous dans l'eau pour les voir devenir d'un rouge intense et franc (à la lumière du jour): la coloration prise est si vive qu'elle résiste même très longtemps à l'action de l'ammoniaque! En outre, après lavage à l'ammoniaque, ils se montrent faiblement, mais incontestablement pseudo-amyloïdes, et, par ces deux caractères, ils se rapprochent donc beaucoup de ceux des *Chaetocalathus* (surtout *C. Craterellus*). Quant à la spore, amygdalaire, non amyloïde, elle évoque d'assez près celle d'*Omphalia candida* BRES. et *Mairei* GILBERT, ce qui confirme que les affinités de cette *Cyphella* sont orientées en direction des *Marasmiacées*.

Cette affinité se confirme et se précise, si l'on étudie les *C. lactea* BRES., *albomarginata* PAT. et *lactea* FR. SS. PAT.

C. lactea a des spores tout à fait semblables à celles de nombreuses *Omphalia* et *Marasmius*, longuement claviformes ou larmiformes, et l'on sait que cette silhouette sporale très caractéristique ne se retrouve guère chez les *Agaricales* ailleurs que parmi les *Marasmiacées*. En outre, le carpophore de cette espèce est pourvu de poils non métachromatiques terminés par une tête arrondie, et qui ne diffèrent guère de ceux de *Delicatula cephalotricha* (Joss.) ČEJF, et d'une forme inédite de *Delicatula Mauritanica* (R. MAIRE) ČEJF, que nous avons découverte sur *Polystichum Filix mas*. Rappelons qu'en outre, l'hymenium de cette *Cyphella* est rugueux.

Avec *C. albomarginata*, la forme en cuiller du réceptacle est déjà bien proche des *Agarics*, et nous lui avons trouvé de jolis poils à parois épaisses, branchus et diverticulés, assez fortement métachromatiques au Bleu de Crésyl, qui ont une évidente ressemblance avec les hyphes dites « en brosse » d'innombrables *Mycènes* et *Marasmes*, et surtout avec les poils des *Delicatula crispula* (QUÉLET) ČEJF et *pseudo-crispula* (KÜHNER). De plus, la trame est constituée par de très grosses hyphes ventruës, dépassant 30

μ de diamètre, comme chez beaucoup de Mycènes, et nous n'en connaissons pas de semblables chez toutes les Aphyllophorales.

C. laeta a une spore larviforme, à fort crochet hilare, qui est exactement une spore de *Marasmius* du groupe *ramealis*. Cette ressemblance se trouve renforcée par les caractères des poils de la cupule, qui sont bouclés, incrustés d'un pigment de membrane, et terminés par de courts bourgeonnements obtus qui rappellent les poils marginaux de *Marasmius languidus* (Fr. ex LASCH) et de plusieurs autres *Marasmius* ou *Collybia* marasmioides (*confluens* Fr. ex PERS., *dryophila* Fr. ex B.); sur le bord de la cupule, on observe même de petits poils rétrécis en col court au sommet, assez analogues aux cheilocystides de *Marasmius epiphyllus* Fr. ex PERS. par exemple. Les hyphes de la chair, molles, très longues, achèvent de donner l'impression qu'on a affaire à une plante relativement voisine des *Marasmius* « *Ramealini* » KÜHNER; nous avons dit d'ailleurs plus haut que son hymenium n'est pas parfaitement lisse, et son carpophore est au début nettement « nuant », presque en forme de pipe.

Avec les *Glabrotricha* PILÁT du groupe de *Cyphella Bloxami* PILÁT (= *C. ciliata* Fr. sensu BOURDOT-GALZIN), une autre affinité se révèle: la spore de cette espèce, et d'une forme lignicole très voisine, un peu plus grande, recueillie par nous sur écorce de *Salix* sp., se montre finement verruqueuse; lorsqu'elle se collapse et se vide de son contenu, elle prend une couleur jaune d'or, et rappelle de façon frappante celle d'une petite Pleurotacée, *Dochmiopus pubescens* ss. SCHRÖTER; cette parenté est confirmée par l'absence de boucles aux cloisons des hyphes, et surtout par la quasi insensibilité de leur paroi au Bleu de Crésyl: en effet, c'est là un des caractères les plus intéressants que nous connaissions chez les *Dochmiopus*; il les oppose aux *Pleurotellus* blancs du groupe *candidissimus* Bk., qui, comme la plupart des *Clitopilus*, ont les hyphes puissamment métachromatiques. L'habitat de ces *Cyphella*, qui poussent sur les feuilles ou le bois, s'accorde en outre avec celui des *Dochmiopus*.

Un tout autre groupe de Pleurotacées — car cette famille manque beaucoup d'homogénéité — paraît aussi toucher à certaines Cyphellinées. *Solenia poriaeformis* (D.C.) rappelle par sa silhouette tubiforme et sa couleur grise une forme très affine (ou même identique) à *Scytinotopsis Kavinii* PILÁT, que nous avons récoltée sur éclat de bois, et cette ressemblance est tout aussi grande au microscope, qui laisse voir un tissu très spécial, d'aspect flou, partiellement coloré de brun (vers l'extérieur, le pigment est clairement incrustant), ainsi qu'une spore arrondie, exactement comme chez *Scytinotopsis Kavinii* et son groupe. On retrouve d'ailleurs à l'extérieur de la cupule de cette *Solenia* des hyphes en cornes de cerf, à bourgeonnement obtus, comme notre *Scytinotopsis* nous en avait lui-même montré. Les relations des *Solenia* grises avec ces Pleurotacées sont donc particulièrement évidentes.

Cependant, toutes les *Solenia* sont loin d'être dans le même cas, car des espèces comme *S. candida* Fr. ex PERS., ou *anomala* Fr. ex PERS. ne nous ont, par leur structure, rappelé clairement aucun groupe d'Agaricales connu de nous; leurs affinités exactes seront probablement très difficiles à établir, mais d'ores et déjà il est permis de douter de l'homogénéité du genre *Solenia*.

Ces ressemblances nombreuses entre *Cyphella* et Agaricales nous ont amené à rechercher la position systématique des *Phaeocyphella*, caractérisées, on le sait, par leurs spores colorées. Nous n'avons malheureusement recueilli vivante aucune espèce de ce genre, mais les exemplaires qui figurent dans l'Herbier BOURDOT sous le nom de *Phaeocyphella muscicola* (Fr.) sensu REA (det. C. COOL, leg. SCHWEERS) et *Ph. musciigena* Fr., nous ont montré des spores fort semblables à celles des *Galerina* par leur couleur jaune un peu rouillé (surtout dans l'ammóniaque, mais la réaction n'est pas aussi nette que chez ces dernières) leur périspore membraneuse recouvrant des verrues obtuses probablement épisporiques, leur plage supra-hilaire nettement limitée et nue, ou moins ornée, leur endospore très nettement colorée. Or, ces caractères

tères, ou plus précisément leur conjonction, sont particuliers aux Agaricales, et ne se retrouvent chez aucune Aphyllophorale, du moins à notre connaissance; ils sont au contraire courants chez de nombreuses Naucoriacées, et permettent donc d'envisager certains rapports entre *Phaeocyphella* et *Agaricus* chromosporés. En outre, l'habitat muscicole de *Ph. muscigena* se retrouve chez un nombre important de *Galerina*.

Les analogies des Cyphellinées avec les Agaricales sont donc trop nombreuses, trop diverses et trop précises pour qu'il soit permis de douter de leur véritable position systématique; elles apparaissent comme un groupe assez hétérogène, et beaucoup sont inséparables de plusieurs familles de champignons à lamelles: Marasmiacées (*Chaetocalathus*, *Delicatula*, *Marasmius*), Pleurotacées (*Dochmiopus*, *Scytinotopsis*) et même Naucoriacées (*Galerina*).

Cette conclusion n'infirme d'ailleurs pas *ipso facto* une certaine parenté des Cyphellinées avec les Corticinées. L'homogénéité de la tribu des Phylactériées, qui réunit pourtant des champignons crustacés (*Tomentella*), odontioïdes (*Caldesiella*) et piléolés (*Sarcodon*, *Calodon*), a été depuis longtemps démontrée, malgré d'énormes différences dans la forme des réceptacles. Il existe d'ailleurs des analogies étonnantes entre d'autres Corticinées et des groupes supérieurs d'Agaricales: c'est ainsi que, chez certains *Gloeocystidium* à spores amyloïdes, on retrouve, comme on le sait, des cystides laticiféroïdes à aldéhydes noircissant ou bleuisant à la Sulfovanilline, comme chez la plupart des Astérorporées agaricoïdes ou gastéroïdes. Et *Gloeocystidium furfuraceum* (BRES.) V. HOEHN., ainsi que *contiguum* (KARSTEN) BOURD.-GALZ. ont des spores à verrues amyloïdes avec plage supra-hilaire nue, au milieu de laquelle on observe une petite tache amyloïde, exactement comme chez les Russules et les Lactaires. Certes, des études très précises et très poussées sur la structure sporale et anatomique de ces champignons devront être entreprises pour dégager la valeur exacte de ces rapprochements, qui ont quelque chance d'être tout fortuits ou dus à des phénomènes de convergence morpho-

logique. Mais les travaux de R. HEIM et de R. KÜHNER ont montré, qu'en culture pure, chez certains Agarics, des basides pouvaient apparaître directement sur le mycelium (*Armillariella mellea* (FR. ex VAHL) KARSTEN), et même qu'il s'y formait parfois des cystides (*Alnicola*). L'hypothèse que parmi les Corticinées, se cachent des formes imparfaites ou primitives d'Agaricales ne peut donc être rejetée *a priori*. Une relation entre les Cyphellinées et ces dernières n'a donc rien qui puisse paraître invraisemblable à un Systématicien d'aujourd'hui. Les belles recherches de CORNER sur les Clavariacées pourraient d'ailleurs conduire, pour cette famille, à des conclusions analogues.

Présenté par M. HEIM.

M. LANGE (Köbenhavn)

The Concept of Species in the Genus Coprinus

Recent monographs on agarics are based on a relatively narrow species concept. It is necessary to study whether these restrictions keep the concept in accordance with that used in other plant groups.

It has been tried to clarify this by studying intersterility and geographical distribution of a group of closely related units in *Coprinus*. The study is based on confrontations of tests from 200 collections belonging to the *Coprinus ephemerus* section. Interfertility is registered by production of clamp connections and/or fruiting bodies. In the material both homothallic and heterothallic, bipolar and tetrapolar types are found, tetrapolarity being most frequent. Some strains produce both homothallic and heterothallic mycelia from one fruiting body. Tetrapolarity often tended towards bipolarity, the combinations identical in the A-factor producing fully normal clamp connections in a narrow zone. Such combinations remained sterile.

Different mating types of two strains were generally all interfertile or all intersterile. In some cases one or two sex-factors were common to two or more strains. In a single case a factor

different from the sex-factors made 2 strains partly intersterile.

Confrontation of the strains divided the material in 22 intersterile groups, the macroscopical and microscopical characters of which were studied and found homogeneous in each group.

14 of the groups fruited in culture. Coprobious habitat was found a distinguishing character. Most groups had characteristic colors, some few characteristic size or taste. Also the rate of deliquescence was distinctive. Consequently many groups could be recognised macroscopically. Clamp connections were constantly absent in 5 groups, present in the rest. Other mycelial characters were but rarely found distinctive. Most groups could be recognised on size and shape of spores. In some the spore size varied much when different fruiting bodies of the same strain were studied. Some groups had distinctive cystidial characters. 2-spored strains were homothallic, aberrant heterothallic mycelia of these were never interfertile with 4-spored strains.

When combining macroscopical and microscopical characters, the groups were generally well characterized as distinct species, the number of which surpassing what is on present record. Some few may be regarded as subspecies. Interspecific hybrids were never met. The material was brought together from distant localities in Europe and America. Each foreign strain was interfertile with a corresponding group in the Danish material. This further supports the concept of the intersterile groups as distinct species, to which a wide geographical distribution is ascribed.

Discussion

E. M. WAKEFIELD: I was very interested to hear that Mr. LANGE found that *Coprinus* forms with 2-spored basidia were intersterile with forms which have 4-spored basidia but are otherwise similar. 2-spored forms occur in other genera of Agarics as *Mycena*, *Hygrophorus* etc. and are often regarded as distinct species, but

by some authors doubt has been cast on the value of this character for specific differentiation. It may be that similar experiments will prove that the 2-spored character is a good one. In the lower Basidiomycetes the number of sterigmata on a basidium may be 2, 4, 6 or even 8 in the same species.

L. E. WEHMEYER: There have been instances of two-spored races of *Coprinus* which were inter-fertile with four-spored races. SASS reported a two-spored race, which was homothallic, of a species normally four-spored and heterothallic. This illustrates again that generalizations are difficult to make, and each case must be considered on its own merits.

M. LANGE: Two-spored strains were found not only intersterile with the related four-spored strains, but also distinct in several, though small, morphological characters. They seem to be specifically different.

R. SINGER: It is rather a coincidence that it was Dr. LANGE's father JAKOB E. LANGE who was one of the first to stress the taxonomic importance of the sterigma number in Agarics, and Dr. M. LANGE himself shows examples where two- and four-spored forms are intersterile and cannot be considered anything but species; this, after this character had been generally minimized in mycological literature.

LILIAN E. HAWKER (Bristol) *Some British Hypogaeous Basidiomycetes*

The collection of hypogaeous fungi has been largely neglected in England since the time of BERKELEY and BROOME. Collections made by BROOME in the west of England were reported in "Notices of British Fungi," published from 1848-85. Many of his specimens were collected in and around Bristol and Bath or in the neighbouring countryside of Gloucestershire and Somerset.

Collections have been made during the last eighteen months, chiefly in the Cotswold beechwoods around Wotton-under-Edge, in the mixed woodlands of Blaise Castle, Bristol, and in North

Somerset, but also as far afield as South Devon and Oxfordshire.

Species Collected

Hymenogaster tener was found most frequently. Nine collections of this fungus have been made since November 1949. Six of these were made under evergreen oak (*Quercus Ilex*) and are all strikingly similar with 2-spored basidia. The remaining three collections were made under beech. Two of these had slightly smaller spores and the second had a proportion of 3- and 4-spored basidia. The spores of this last specimen developed in succession on a particular basidium instead of simultaneously as in all other collections. W. G. SMITH figures basidia of *H. tener* with four spores at a similar stage. The specimen under consideration indicates one way in which a 4-spored form might give rise to a 2-spored variety by an increase in the time-interval between the development of successive spores of a basidium leading to the suppression of the last two spores.

These collections illustrate some of the difficulties in taxonomic work with hypogaeous fungi. Slight differences between collections suggest that the species are still plastic and liable to change. These differences may be correlated with the particular tree with which a strain is associated. Thus the collections of

H. tener fall into two groups, a uniform group of six collections from under evergreen oak and a less uniform group from under beech.

Collections were also made of *Hymenogaster luteus*, *Gautieria graveolens*, *Hysterangium nephriticum*, *H. Thwaitesii*, *Rhizopogon rubescens*, *Melanogaster ambiguus*, *M. variegatus* and *Sclerogaster compactus*.

The most interesting species is one of which three collections have been made at widely separated spots in the same Cotswold beech wood at Wotton-under-Edge. Specimens which varied from 0.5–2.5 cm diameter were attached to a definite rhizomorph and possessed a thin, wrinkled, dirty white peridium, splitting when mature to show the gleba. The latter is flesh-coloured in young specimens and becomes purple-brown in older ones. The cavities are small and air-filled and develop first at the centre leaving sterile pockets at the base and at the periphery but eventually the whole gleba becomes differentiated. The basidia are 2-spored and the spores themselves are spherical when mature, golden brown, with a dimpled or pitted wall and a colourless papilla at the point of attachment to the basidium. The systematic position of this fungus was discussed in detail and it was concluded that, while it is not closely similar to any known species it may best be placed provisionally in the genus *Sclerogaster*.

SESSION 4

Jointly with Section TCR: July 17th, 9 a. m. — noon

Chairman: R. HEIM, Recorders: J. A. NANNFELDT and N. FRIES

SUBJECT:

Phylogeny and Systematics of Phycomycetes

RALPH EMERSON (Berkeley, Calif.)

Experimental Investigations of the

Physiology, Cytogenetics, and Cytotaxonomy of the Blastocladiaceae

Investigations designed to elucidate the basic mechanisms of sexual reproduction in the aquatic Phycomycete *Allomyces* have shown

that we can only reach this goal by a fuller understanding of the overall biology of the genus and its close relatives, *Blastocladiella* and *Blastocladia*. The point can be illustrated by a review of recent advances in our knowledge of the physiology and nuclear cytology of the Blastocladiaceae.

Comparative studies of *Blastocladia Prings-*

heimii (CANTINO, 1948-49) and *Allomyces* sps. (INGRAHAM, unpublished) have furnished information on the vitamin nutrition, carbohydrate utilization, oxygen requirements, and metabolic processes of these fungi and, hence, have permitted controlled investigation of the formation and behavior of their reproductive structures, have made it possible to interpret the nutritional characteristics of interspecific hybrids, and have provided the basis for research (MACHLIS, unpublished) on induced mutations and their possible effect on sexual processes in *Allomyces*.

WILSON's demonstration (1948 and unpublished) of meiosis in the germinating resistant sporangia of *Allomyces* has established the extent of diploidy in the three subgenera. Further studies of meiosis in hybrid strains have explained the reduced fertility of the F₁ generation and the inheritance of the sex-determining mechanism, while chromosome-counts of the various species and hybrids have given clues to their origins and relationships.

HILDA M. CANTER-LUND (Ambleside) *Planktonic Phycomycetes*

Although there are isolated accounts of fungi which occur as parasites and saprophytes on the phyto- and zooplankton no intensive survey of these organisms has previously been undertaken. Studies on lakes in the English lake district and elsewhere by the writer, have shown that there is a rich and varied fungal flora to be found in this habitat. Even up to 71 % of the common plankton algal species (e.g. in Windermere) may be infected by fungi during one or more periods of the year. Numerous algae have more than one parasite or saprophyte, some as many as four different species. The majority of the fungi which occur on the phytoplankton belong to the Chytridiales but there are also a few biflagellate forms. Several polyphagoid chytrids occur on colonial algae in which the individual cells are embedded in a mucilage envelope or joined together to form a filament.

The fungi which have been found so far as

parasites on the zooplankton all belong to the Biflagellatae. Uniflagellate fungi belonging to the well known group of exuviaceous chytrids often occur in the empty bodies of Crustaceans and Rotifers. Very few chytrids have been encountered which cause hypertrophy of the algae host cells. Parasitism among the Uniflagellate fungi themselves is not uncommon.

At certain times many of the fungi multiply rapidly to epidemic proportions. With the collaboration of Dr. J. W. G. LUND for the past three years quantitative work on the Desmids and the diatoms, *Asterionella* and *Fragilaria*, has shown that parasitism may be considered as an important biological factor in relation to changes in numbers of these organisms and of the phytoplankton in general.

GRACE M. WATERHOUSE (Kew)

Identification of Phytophthora Species by Means of Oospores Produced in Dual Cultures

The genus *Phytophthora* includes species which appear to be truly aquatic and can grow for a long time and reproduce readily in water, even when conditions are sub-optimal. Until 1940 these *Phytophthora*-like water moulds were usually placed in PETERSEN's genus *Pythiomorpha*, now regarded as synonymous with *Phytophthora*.

P. megasperma DRECHS. was the first to be recognized as a water mould as it produces oospores readily. The author has identified two isolates of this species received from aquatic habitats in Great Britain. Identification of the other species did not appear possible as they rarely, if ever, produced oospores. Recently, however, oospores have been obtained in quantity in a short time by culturing the unknown water mould in company with known *Phytophthora* spp. In this way it has been possible to identify water moulds, which appeared from their vegetative characters to resemble *P. cryptogaea* PETHYB. & LAFF., by growing each with *P. cinnamomi* RANDS. (sub-culture of RAND's original isolate from C. B. S.), numerous

oospores developing in 10 days. Present in the dual culture were two types of oogonium and oospore: small, ranging from $22\ \mu$ to $28\ \mu$ (oogonium) in diameter, typical of *P. cryptogea*, and larger ones $29\ \mu$ to $37\ \mu$ or more, typical of *P. cinnamomi*. When *P. cinnamomi* was grown in company with *P. palmivora* BUTLER (rubber group) again there were two distinct types of oogonium and oospore in the culture, oogonia typical of *P. palmivora* being around $30\ \mu$ and those of *P. cinnamomi* as before.

Water moulds resembling in vegetative characters *P. cambivora* (PETRI) BUS. have occasionally been encountered and it was considered worth while to investigate the pairing possibilities of this species, which rarely produces oospores in pure culture. A subculture of PETRI's original isolate from C. B. S. produced no oospores in pure culture, nor did it do so when grown with *P. cryptogea* or *P. cinnamomi* or *P. palmivora*. With *P. parasitica* DAST., however, oospores were produced in quantity in five days. Again there were two different types: one was small and typical of *P. parasitica* with oogonia on the average $25\ \mu$ in diameter; the other was quite distinct, the oogonia were $40\ \mu$ or more and the wall was erupted with a variable number of papillae. This type of oogonium has been described by previous workers as that of *P. cambivora*. Two other isolates of *P. cambivora* behaved in the same way when grown with *P. parasitica*. Moreover, the two types of oogonium were secured when *P. cambivora* was grown with either of the two complementary strains of *P. parasitica*. Thus it seems possible to distinguish *P. cinnamomi* and *P. cambivora* on these grounds, the former having a smooth oogonial wall and developing oospores in culture with *P. cryptogea* and *P. palmivora*, but not with *P. parasitica*, and the latter having a papillate oogonial wall and developing oospores only with *P. parasitica*.

From the above evidence it appears that *P. cambivora* is basically hermaphroditic and that either *P. cinnamomi* or *P. cryptogea* is hermaphroditic or possibly both are. Evidence has also been obtained that one strain of *P. para-*

sitica is basically hermaphroditic as it can be induced to produce oospores in single strain culture. It seems highly probable that all species of *Phytophthora* may prove to be basically hermaphroditic and that the necessity for using two strains for the production of oospores is not because the species is heterothallic but because some biochemical stimulation is required; this might be provided by some other means.

MINA NADEL-SCHIFFMANN (Rehovot)

L'influence de la température et de la pluviosité sur l'apparition des différentes espèces de Phytophthora

Des observations sur les fruits des Agrumes ont été faites pendant plusieurs années, durant la saison de la cueillette de ces fruits, à savoir depuis le mois de novembre jusqu'au mois d'avril. Ces observations portaient sur les relations qui existent entre la quantité des pluies et la température d'une part, et la quantité des fruits affectés par différentes espèces de *Phytophthora* trouvés en Israël d'autre part.

Cette étude montre que la quantité de pourriture des fruits des Agrumes, provoquée par *Phytophthora* en une année quelconque, dépend de la quantité et de la distribution des pluies tombées pendant la saison, depuis novembre jusqu'en avril.

D'autre part l'espèce de *Phytophthora* qui cause la pourriture brune des fruits durant la saison, dépend surtout de la température de l'air pendant cette époque.

L'apparition des différentes espèces de *Phytophthora* durant la saison, est en relation avec leurs diverses exigences envers la température in vitro.

Ainsi l'espèce de *Phytophthora citrophthora* qui s'accommode à une échelle de température assez large (l'optimum est d'environ de 25°C . La croissance des champignons se produit assez vite entre les températures de $15-30^{\circ}\text{C}$.) apparaît en grande quantité presque pendant toute la saison des fruits. C'est surtout le *Phytophthora citrophthora* qui pendant des an-

nées très pluvieuses provoque un épiphytotoxie des Agrumes.

L'espèce de *Phytophthora parasitica* ayant comme optimum de croissance in vitro une température assez élevée (32° C), a été trouvée dans les fruits pourris seulement durant la partie de la saison des fruits où la température de l'air est assez élevée. Ces conditions se réalisent seulement au commencement et à la fin de la saison des fruits, c'est à dire, vers les mois de novembre-décembre, ou bien vers le mois d'avril.

L'apparition de l'espèce de *Phytophthora hibernalis* qui a comme optimum de croissance in vitro, une température très basse (20° C), le maximum 23° C, croît encore assez bien à la température de 6° C. Cette espèce a été trouvée durant la saison seulement aux périodes de température basse.

Cette étude peut avoir une importance plus générale pour les recherches sur l'apparition des maladies en relation avec le climat. Ainsi apparition d'une certaine maladie peut avoir lieu dans n'importe quel climat (même l'apparition de *Phytophthora hibernalis* dans le climat subtropical d'Israël), si les conditions exigées par ces champignons s'y réalisent au moins pendant une certaine période de temps.

M. T. COOK (Baton Rouge, La.)

The Distribution of Species of the Genus Synchytrium in North America

About 95 species of the genus *Synchytrium* have been described. The descriptions of 43 species are incomplete but are sufficient to place them in this genus. About 59 species have been reported from North America including the West Indies and Greenland. Most of the North American species have been reported from the United States but the descriptions of 13 of them are incomplete. 14 of the North American species were described first in Europe, one in South America, one from Costa Rica and one from Greenland. The species said to be common to both Europe and North America are:— *S. Andium*, *S. anemoneum*, *S. anomalum*,

S. aureum, *S. Chrysosplenii*, *S. endobioticum*, *S. fulgens*, *S. globosum*, *S. myosotidis*, *S. plantageum*, *S. potentillae*, *S. Stellariae*, *S. Succisae* and *S. Taraxaci*. The majority of the North American species have been reported from one of four areas—the eastern, the middle west, the southern and the Pacific coast areas. The writer doubts if any of the 14 species is the same as those in Europe where they were described first. The literature indicates that the great majority of species attack but one species of host plants, that a very few species attack two genera and that a very few attack more than two genera. *Synchytrium aureum* appears to be an exception. It has been reported as attacking 197 species in 127 genera and in 31 families. This is very doubtful. The writer believes that several species have been included under the name *S. aureum*. Color is of very little value in writing descriptions and making determinations. It varies with age. The four characters most satisfactory in writing descriptions are size of fungus just before the formation of zoosporangia, formation of sporangia, number of sporangia and structure of galls. The writer believes that many of the specimens in the American herbaria have been determined incorrectly. Also, the writer is doubtful that all of the 14 species originally described in Europe and later reported in America have been determined correctly. The writer requests European material of these 14 species that have been properly killed and embedded in paraffin for sectioning so that comparisons can be made.

JOHN T. MIDDLETON (Riverside, Calif.)

Peronosporaceae of the Colorado Desert of California, U.S.A.

Ten species of *Peronospora* and one species of *Plasmopora* were collected in the winter of 1940–41 in the Colorado desert of California. They have not been observed since despite the presence of adequate annual vegetation and repeated searches for them.

The Colorado desert is isolated by a mountain barrier ranging from 3000 to 10 000 feet in

elevation and the Gulf of Baja California. The desert floor varies from 200 feet below sea level to 400 feet above. The mean annual rainfall of about 3 inches falls largely from November to May and is heaviest in December. Analysis of the available weather data indicates that the single occurrence of the fungi is associated neither with above normal rainfall nor the number of cloudy days, but is related to the number of days with rain of 0.01 inch or more and especially with the number of rainstorms within seven days of a succeeding rainstorm. The occurrence of the two latter conditions once the native flora is developed not only extends the life of the vegetative period but apparently provides an environment assuring the production of sporangia, their dispersal, germination, and subsequent host infection.

The following are the fungi and their hosts, of which thirteen genera and eleven species are newly recorded as susceptibles: *Peronospora alta* FCKL. on *Plantago insularis* EASTW.; *P. arthuri* FARL. on *Oenothera brevipes* GRAY, *O. Cardio-phylla* TORR., *O. scapoidea* T. and G.; *P. Claytoni* FARL. on *Calyptridium monandrum* NUTT.; *P. echinospermi* SWINGLE on *Cryptantha holoptera* (GRAY) MCBR., *Plectocarya penicillata* (H. and A.) A. DC., *Plagiobothrys Arizonicus* (GRAY)

GREENE; *P. effusa* (GREV.) DEBY. on *Atriplex canescens* JAMES, *Chenopodium murale* L.; *P. Hydrophylli* WAITE on *Emmenanthe penduliflora* BENTH., *Nama demissum* GRAY, *Phacelia crenulata* TORR., *P. tanacetifolia* BENTH.; *P. oxybaphi* ELLIS and KELLERM. on *Abronia villosa* WATS., *Mirabilis tenuiloba* WATS., *P. parasitica* (PERS.) DEBY. on *Dithyrea Californica* HAW., *Draba cuneifolia* NUTT., *Lepidium flavum* TORR., *Sisymbrium pinnatum* (WALT.) GREENE *Tropidocarpum gracile* HOOK., *P. tabacina* ADAM on *Nicotiana trigonophylla* DUNAL., *P. trifoliorum* DEBY. on *Astragalus nuttallianus* DC., *Hoffmanseggia microphylla* TORR., *Lotus rigidus* (BENTH.) GREENE, *Lupinus shockleyi* WATS.; *Plasmopara halsedi* (FARL.) B. and DT. on *Geraea canescens* T. and G.

The source of all the fungi enumerated is not known. Despite the isolation of the Colorado desert and the possibility of an endemic fungus flora, two fungi, namely *Peronospora tabacina* and *P. hydrophylli*, apparently gained entrance from their usual coastal habit by means of susceptibles distributed upon the mountain barrier. It is suggested that some of the fungi may have inhabited the area at an earlier date since co-spores of the other fungus species have been found in infected plant tissue.

SESSION 5

July 17th, 1—3 p. m.

Chairman: J. RAMSBOTTOM, Recorder: N. FRIES

SUBJECT:

Medical Mycology. Bacteriology

CH. W. EMMONS (Bethesda, Md.) *The Natural Occurrence in Animals and Soil of Fungi which Cause Disease in Man*

The systemic mycoses or deep fungous infections of man are noncontagious and are transmitted from person to person only in rare cases. This is generally recognized as an important factor in the epidemiology of mycoses. A corollary of this principle is that the fungi

causing these mycoses may have an independent saprophytic existence in man's environment.

There is a sound basis for the hypothesis that pathogenic fungi capable of causing human and animal disease are more commonly present in soil and vegetation than mycologists generally realize. Frequently mycotic infections have developed after an accident in which there was opportunity for the introduction of fungus spores through a puncture wound of the skin

or after the inhalation of dust which may have been contaminated by spores. Finally, pathogenic fungi have actually been isolated from soil and vegetation. The first line of evidence is circumstantial, but convincing, while the second is conclusive.

Mycetomas of the Madura foot type, sporotrichosis, and chromoblastomycosis are examples of mycoses which can be associated in many instances with trauma. Mycetoma of the foot is seen most frequently in tropical and subtropical countries in persons who work barefoot in the fields and are subject to occasional puncture wounds of the feet. In many instances the patient can give a history of such an accident which shortly preceded development of the infection. Mycetoma, which has a multiple etiology, is occasionally caused by one of the partially acid-fast species of *Nocardia*, which are known to be present in soil. Chromoblastomycosis likewise is most often seen in farm laborers who are exposed to injury by thorns and splinters (3). Sporotrichosis also occurs in persons exposed to soil and plants. It is seen in gardeners, and compensation for cost of medical care has been awarded by the courts in cases where an employment-connected disability was recognized (11). Infection has been attributed in specific instances to implantation of spores in puncture wounds by thorns (11) of barberry, rose, and other thorny plants, and to injury by contaminated mine timbers (2). The proved occurrence of *Sporotrichum Schenckii* on plants and timbers will be discussed in a later paragraph.

Inhalation of windblown spores of *Coccidioides immitis* is well established as the cause of most cases of coccidioidomycosis (18). Infection may follow exposure to dust storms or exposure in such occupations as picking dusty cotton or grapes, building roads, or working in the fields within the endemic area of this disease (19). Aspergillosis is another pulmonary mycosis in which an occupational exposure has sometimes been recognized (17).

Several of the fungi which cause disease in man also cause naturally acquired mycoses in

animals. Strains of *Actinomyces bovis* (A. ISRAELI) similar to bovine strains are found in at least some of the cases of human actinomycosis (23). *Sporotrichum Schenckii* causes sporotrichosis in the horse and dog (15). *Coccidioides immitis* causes disease in the dog and rodents and induces a limited infection in cattle and sheep (5, 8, 21). *Aspergillus fumigatus* produces aspergillosis frequently in birds (17). Although these systemic mycoses are common to man and animals it is very doubtful whether there is direct transmission from one to the other except in rare and accidental cases. The relationship is different in the case of the superficial dermatophytoses in which animals such as horses, cattle, dogs and cats appear to be the direct source of human infection in many cases. Laboratory workers may be infected from mice, monkeys and other laboratory animals following exposure.

The mycologist may be more interested in the actual proved presence in soil or on vegetation of fungi capable of causing human disease, than in the circumstantial evidence for their presence cited above. Undoubtedly the pathogenic fungus most often found in soil and decaying vegetation is *Aspergillus fumigatus* (22). The relative infrequency of human infection probably indicates a high degree of resistance to infection, for exposure must be very frequent and sometimes heavy. In one of the early searches for pathogenic fungi in nature BEURMANN and GUGEROT found *Sporotrichum Schenckii* growing on the bark of beech, on *Equisetum*, and on oats hay, and made three isolations from these sources (1). A very remarkable occurrence of *S. Schenckii* on the timbers of gold mines in South Africa was reported by BROWN et al. (2). The fungus was present in considerable quantity and was responsible for many infections in the native miners. MEYER (15) discussed the probable role of soil contamination in a paper on the relationship of animal to human sporotrichosis. MACKINNON (14) made a careful study of the seasonal occurrence of sporotrichosis and correlated this with climatological conditions

which, he believed, favored the saprophytic development of the pathogenic fungus. The writer has isolated *S. Schenckii* from *Sphagnum* moss associated with a small epidemic among florists (12).

CONANT (25) showed that *Cadophora americana* isolated from wood is the same as *Phialophora verrucosa* which had been described previously from chromoblastomycosis.

Coccidioides immitis has been isolated from soil from three areas in southwestern United States, (20, 4, 5) and it is generally recognized that exposure to wind-blown soil is an important factor in the epidemiology of coccidioidomycosis. Although the presence in soil of *Coccidioides* is generally admitted, the factors limiting it to a relatively small geographic area are not yet fully known.

The great abundance of *Streptomyces* and other actinomycetes in soil is well recognized. The acid-fast species, *Nocardia asteroides*, has been isolated from soil and its pathogenicity proved by animal inoculations (13). The presence of dermatophytes in stables where infected animals were kept has been reported (16), and *Microsporum gypsum* has been isolated from soil, where there was no obvious contamination by animals, by "baiting," i.e., by burying wool in soil where it served as a differential culture medium for the isolation of wool-destroying fungi (24).

Thus it is apparent that the natural occurrence of pathogenic fungi in soil, which can be postulated to account for the observed peculiarities of the epidemiology of the mycoses, is well substantiated by the actual isolation of several pathogens of man from such natural substrates as soil and decaying vegetation.

The writers attention was directed to this problem during a study of coccidioidomycosis in which *Coccidioides immitis* was isolated from 5 of 150 soil samples collected in Arizona (5). In that study also, the fungus was isolated for the first time from pulmonary lesions in pocket mice and other desert-dwelling rodents (8). In more recent studies made in this laboratory (6, 6a, 7, 9, 10) *Histoplasma capsulatum* was

isolated for the first time from the brown rat, roof rat, house mouse, spotted skunk, opossum, and cat, and from soil (6). Incidental to those studies several other fungi have been isolated from animals or soil and since some of these are pathogens and some have not been reported previously from the sources cited the observations are herewith recorded.

Sporotrichum

In addition to isolations of *Sporotrichum Schenckii* mentioned above the writer has isolated this fungus once from the liver of a pine mouse (*Pitymys nemoralis*) collected near Keosauqua, Iowa, September 5, 1945. The animal did not appear to be ill and no lesions were observed when the organs were examined after the animal was killed. The evidence for infection rests wholly upon the isolation of the fungus in culture from the liver. This fungus was isolated again indirectly from soil collected near Lucketts, Virginia, October 4, 1948. The soil specimen was taken from the edge of a building where maize was stored, on a farm where rats with histoplasmosis had been collected previously.

Since most of the pathogenic fungi grow slowly it is impracticable to attempt their direct isolation from soil where the spores of rapidly growing fungi are also present. The method used in this and other cases in which pathogenic fungi were isolated from soil was to make a suspension of the specimen in physiological salt solution and inject this into white mice. The animal is then killed after an interval of 4-6 weeks and cultures are made from the liver and spleen. At the time this isolation from soil was made no animals with experimental sporotrichosis were kept in the laboratory and spontaneous sporotrichosis has not been observed in our animal colony. It is therefore believed that the indirect isolation indicates the actual occurrence and growth of the pathogen in soil.

Trichophyton

The literature contains an occasional reference to the isolation of *Trichophyton* from

the circulating blood of human patients with dermatophytosis (ringworm). It is assumed in these cases that when the infection is somewhat more deep-seated than usual a hyphal fragment occasionally gets into the blood stream. It is interesting in the light of these old observations that a fungus which appears to be a typical strain of *Trichophyton mentagrophytes* has been isolated on several occasions from the visceral organs of animals in which dermatophytosis was not observed. This fungus was isolated from the lungs of a kangaroo rat (*Dipodomys Ordii*) caught near Lordsburg, New Mexico, September 9, 1942; from liver and spleen of two white-footed mice (*Peromyscus maniculatus*) caught near Keosauqua, Iowa in 1945; from liver and spleen of one *Peromyscus maniculatus* and one house mouse (*Mus musculus*) caught near What Cheer, Iowa in 1945; from the lungs of *Peromyscus* sp. and the short-tailed shrew (*Blarina brevicauda*) caught in Virginia in 1946; from lymph nodes of the neck of an opossum (*Didelphis virginiana*) caught in Virginia in 1950, and from rats (*Rattus norvegicus* and *R. rattus*) caught in Georgia in 1948. Neither gross nor microscopic lesions were found associated with these isolations, and the possibility that they were air-borne contaminants of the cultures was considered. However, the fact that the fungi grew widely over the inoculated culture, the fact that they could be recovered several weeks after reinoculation into experimental animals, and their very close resemblance to *T. mentagrophytes* led to their identification as pathogenic fungi. Experimental studies have not been completed, but some attempts to reproduce dermatophytosis with these strains were not successful. However, it is well known that many similar strains isolated from "athletes' foot" do not readily produce experimental lesions in animals.

Cryptococcus sp.

Over a period of several years records have been made of 105 isolations of a species of *Cryptococcus* from 60 specimens of house mouse (*Mus musculus*), 43 of the brown rat (*Rattus*

norvegicus) and 2 of the meadow vole (*Microtus* sp.). The same fungus has been isolated repeatedly from soil by the indirect method of experimental injection of white mice mentioned above. The fungus has a very low degree of virulence and even when large numbers of cells from a pure culture are injected into an experimental animal no progressive lesions are produced although the fungus can be recovered in culture many weeks after experimental infection.

In culture the fungus forms small white glistening colonies on acid dextrose agar. The cells are spherical or subspherical 4-6 μ in diameter with occasional cells in old cultures reaching 10 μ with a relatively thick wall. They often contain one or more hyaline bodies, presumably glycogen. The fungus ferments levulose, dextrose and mannose with formation of acid and gas. A more complete description of this fungus will be given in a later paper.

Nocardia Pelletieri

Nocardia Pelletieri was isolated from the liver of a mouse (*Mus musculus*) caught in Virginia April 8, 1947. Pathogenicity studies have not been made but the strain appears to be identical with one isolated from mycetoma.

Allescheria Boydii

Allescheria Boydii has been isolated once from the litter in a barn near Taneytown, Maryland. The strain was typical of those isolated from mycetoma of the foot. It was a fertile strain producing numerous ascocarps as well as the conidial stage designated *Monosporium apiospermum*. This is the first time this fungus has been isolated from any source except a human infection.

Miscellaneous fungi

Besides the fungi discussed above several fungi of more than casual interest have been isolated, although no etiological importance is attached to them, and they will be mentioned only briefly. *Rhodotorula* sp. has been isolated once from *Blarina brevicauda*, 11 times from

Mus musculus and 6 times from *Microtus* spp. Many of these animals were dead when brought to the laboratory and it is suspected that *Rhodotorula* is a terminal invader. *Beauveria* sp. has been isolated from the lungs of several species of animals. No lesions were found associated with these isolations, and it was considered that the fungi were represented in the animal only by recently inhaled spores. *Aspergillus fumigatus* was isolated many times from lungs and *A. clavatus* was isolated repeatedly from the lungs of rats. These fungi, also, apparently were merely contaminants of the respiratory passages. When attempts were being made to isolate *Histoplasma* from soil by injecting soil suspensions into mice an interesting finding was the very frequent isolation of *Microascus* spp. from the peritoneal cavity of the experimental animals. These fungi are known as soil inhabitants, but it was interesting to observe that the spores were able survive periods of 6 weeks in the peritoneal cavity of mice without being destroyed.

Summary

The natural occurrence of coccidioidomycosis, histoplasmosis, and sporotrichosis in various species of animals and the isolation of the pathogenic fungi causing these mycoses and of *Allescheria Boydii* from soil indicate that some of the fungi causing mycoses in man have a wide range of host species, and, in some cases at least, an independent saprophytic existence in soil. This is the first record of the isolation of *A. Boydii* from any source except human lesions. A species of *Cryptococcus* and a fungus apparently identical with *Trichophyton mentagrophytes* were isolated frequently from visceral organs of animals under circumstances indicating mild pathogenicity, and *Aspergillus fumigatus*, *A. clavatus*, *Rhodotorula* sp., *Beauveria* sp. and *Microascus* spp. were isolated repeatedly from animals under circumstances suggesting recent contamination of the respiratory passages or, in the case of animals inoculated with soil suspensions, survival without growth in the animal body.

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- investigators have found the dermatophytes growing in stables where infected animals were kept. In soil from which we have isolated *Histoplasma* we have been able to find by direct microscopic examinations conidia of *Histoplasma* which indicates that this fungus has grown saprophytically in soil. *Nocardia asteroides* has been isolated from soil using paraffin as a selective medium. Finally, many of the pathogenic fungi will grow on sterilized soil which has been artificially inoculated.

H. PALDROK (Uppsala)

On the Variability and Classification of the Dermatophytes¹

A. FRISK and P. HEDENIUS (Stockholm)

The Histoplasmin Test as a Diagnostic Aid in Obscure Pulmonary Affections. A Preliminary Report

Clinicians often come across patients with pulmonary lesions of unknown etiology. Tuberculosis would seem to be a likely diagnosis, but it cannot be verified by ordinary diagnostic procedures. Sometimes such changes remain hidden until a routine X-ray examination is made of the chest, when they may be characterized as calcified lymphatic glands. A negative skin reaction to tuberculin does not exclude the presence of tuberculosis: the patient may be transiently anergic. Certain American researchers, however, suggest that there might be another reason for these tuberculin negative pulmonary injuries. Some fungous infections in the lungs may give rise to a tuberculosis-like condition, and some authors claim they have demonstrated secondary calcification of the hilar lymph nodes. It has been found that the patients in question show a positive reaction to skin tests with the corresponding fungous antigen, whereas they often react negatively to

¹ This paper will be published in *Acta Dermato-Venereologica*, Sweden.

Discussion

A. NORDÉN: Have you been able to isolate *Blastomyces dermatitidis* from soil or wild animals?

CH. W. EMMONS: We have not been able to isolate *Blastomyces dermatitidis* from soil or wild animals.

T. W. GROVES: Is there evidence of danger to birds of infection by *Aspergillus fumigatus* as a result of eating infected seed?

CH. W. EMMONS: There is, and it is usually assumed to be the source of infection.

P. H. GREGORY: You have referred to certain pathogenic fungi as having an independent saprophytic existence in soil. Is there good evidence that they do in fact grow and colonize soil, or is it possible that they merely persist as resting spores from an animal source?

CH. W. EMMONS: We believe that some pathogenic fungi are able to grow saprophytically in soil. The reasons for this are as follows: Some

tuberculin. And it has been demonstrated that in certain parts of the U. S. A. there live a high proportion of persons with the constellation: positiveness to histoplasmin (an extract of *Histoplasma capsulatum*) and negativeness to tuberculin.

A corresponding investigation has been considered desirable in Sweden, the primary aim being to ascertain whether any histoplasmin positive Swedes actually exist. Two kinds of histoplasmin were used: one prepared by us according to EMMONS's directives, and another procured from Ely Lilly & Co., Inc. Generally a dilution of 1:100 was used. Our test persons were selected from a group of tuberculin negative patients with obscure pulmonary affections, with or without hilar lymphadenic calcification. None of the test persons were histoplasmin positive. Our group is still too small, however, to warrant the statement that no such persons exist in Sweden. Our work was nevertheless interesting from another point of view. While the antigen was being prepared from *Histoplasma capsulatum* a mild laboratory infection occurred which was productive of reliable information on histoplasmosis—the disease caused by *Histoplasma capsulatum*.

The existence of a benign or subclinical form of histoplasmosis is being debated in the U. S., and we therefore thought it might be valuable to present some facts about the laboratory infection. One of us, who was negative to histoplasmin (1:100) in 1948, in February 1949 had a trivial infection in the upper respiratory tract. It was accompanied by moderate fever, a fair amount of coughing and slight expectoration. The symptoms being attributed to a common cold, no bacteriological study was made, nor were the lungs X-rayed. Full recovery occurred within two weeks. Repeated in July 1949, the histoplasmin test evoked a highly positive reaction, but a simultaneous lung X-ray was negative. Among the other members of the personnel 4 took ill during the summer of 1949 with symptoms of respiratory tract infection. X-ray of the lungs in one case revealed bilateral basal densities and an enlarged right hilus, as well as

negligible exudation on this side. S. R. 42 mm. The pharyngeal flora was normal and the auto-agglutination test (+4 C°) negative. Negative to 1 mg tuberculin intracutaneously. The infection was resistant to penicillin and persisted for several months. Tuberculous tests on guinea pigs and Loewenstein cultures were negative. Some of the pulmonary lesions were still to be seen in the spring of 1950, when a bronchoscopy revealed mucosal swelling in the explorable part of the bronchial system on the right side. There was in addition a subcarinal easily bleeding granuloma. A biopsy revealed that it contained typical tuberculous granulation tissue, but no acid-fast rods could be demonstrated. The patient was still tuberculin negative, but strongly positive to histoplasmin 1:100. A bronchoscopy repeated a month later showed a practically normal condition. A subsequent complement fixation test was positive to histoplasmosis.

All our test persons being negative to histoplasmin, there is no valid reason to assume that the diseased laboratory staff had previously been histoplasmin positive. In one case, moreover, a negative reaction was obtained in 1948. Most probably, therefore, a mild histoplasmin infection was present which healed comparatively soon. Hereby the existence of a benign form of histoplasmosis would seem to be verified.

Å. NORDÉN (LUND)

The Role of Temperature in a Sporotrichum Precipitin Reaction

Summary: Using a polysaccharide and a crude autoclaved antigen from *Sporotrichum Schenkii*, the precipitin reaction was studied at 5.5–8° C, 24° C and 35–36° C with a Libby photron-reflectometer. It was found that during the first few minutes more rapid flocculation occurred at the higher temperatures but that later the fastest flocculation takes place at the lower temperatures.

(To be published in *Acta pathologica et microbiologica scandinavica*).

B. NORÉN (Uppsala)

Methods of Growth-Determination of Myxobacteria

In investigations on *Myxobacteria* it is a difficult problem to determine the amount of growth. The methods of determination reported in the literature are mostly based on subjective ratings.

Regarding the results of the investigations of the bacteriolytic activity of *Myxobacteria* it occurred to the author that it might be possible to determine the lysis photometrically and in the degree of lysis have a measure of the activity of *Myxobacteria*. For this purpose the following method was worked out: A suspension of *Staphylococcus aureus* grown on broth nutrient agar was made in distilled water and distributed in culture tubes. It was previously washed 3 times in distilled water by centrifugation. After autoclaving, the tubes were inoculated with a homogeneous suspension of *Myxococcus virescens* and incubated at +25° C. During the incubation the tubes were mechanically shaken. The decrease of extinction, caused by the bacteriolytic activity of the *Myxobacteria*, was determined in white light by means of the photometer used by ÅBERG and RODHE 1942. By inoculating 4 series of *Staphylococcus* tubes with 0.25, 0.4, 1.0 and 2.0 ml of a suspension of *Myxococcus virescens*, it could be shown that the decrease of extinction within certain limits was directly proportional to the amount of inoculation, that is to the number of *Myxobacteria*. Thus the decrease of extinction may give an idea of the amount of *Myxococcus virescens*.

With this method the activity of *Myxococcus virescens* was examined at different pH values. Nutrient solution used was of the fol-

lowing composition: 5 grams of total acid hydrolyzate of casein, 0.5 g NaCl, 0.333 g *Staphylococcus* cells and 1000 ml distilled water. The pH was adjusted with 0.1 N HCl and 0.1 N NaOH. The pH values examined were 1.9, 2.8, 3.6, 6.0, 6.9, 7.8, 8.7 and 9.6. The time of incubation was three days. A slight but definite decrease of extinction was observed after 7 to 24 hours at pH 2.8 and 3.6. In these two cases as well as at pH 6.0 the decrease seemed to be due to a bacteriolytic substance in the inoculum. Thus, the bacteriolytic substance produced by *Myxococcus virescens* is active within a very wide pH range. The lower pH limit seems to be somewhere between 2.8 and 3.6. The upward limit is apparently not reached at the pH of 9.0. The cells of *Myxococcus virescens*, however, seem to be capable of activity only in neutral and alkaline substrates. A marked optimum for activity appears to exist between pH 6.9 and 7.8. The myxobacteria were active at pH 8.7 and probably even at pH 9.6.

It has been shown that with the above method it is possible to make more detailed observations of *Myxococcus virescens* than has been possible earlier. Preliminary experiments indicate that the method is also suitable for *Myxococcus rubescens*, *Chondrococcus coralloides*, and *Archangium primigenium*.

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SESSION 6

Jointly with Sections CYT and GEN: July 18th, 9 a. m. — noon

Chairman: A. QUINTANILHA, Recorders: N. FRIES, A. LEVAN and A. MÜNTZING

SUBJECT:

Genetics and Cytology of Microorganisms

Ö. WINGE (Köbenhavn)

The Polymeric Genes for Maltose Fermentation in Yeasts, and their Mutability

A considerable discrepancy prevails between the strange mode of inheritance of the genes for sugar fermentation in yeasts proposed by LINDEGREN and his colleagues in the United States and the simple Mendelian form of inheritance which we have observed at the Carlsberg Laboratorium where, in collaboration with Dr. CATHERINE ROBERTS, I have undertaken detailed investigations of the genes for maltose fermentation.

Previously we had demonstrated the existence of 3 maltase genes, M_1 , M_2 , and M_3 , in *Saccharomyces cerevisiae*, and we have now found, by means of induced as well as spontaneous mutation, a fourth maltase gene, M_4 .

Through spore crossings between yeast types, each with a different gene (for example, M_1 and M_2), we have obtained doubly heterozygotic hybrids, the asci of which yielded typical 2-gene segregations. Crossings between a yeast type containing one maltase gene and a complete recessive have resulted in the production of hybrids, the 4-spored asci of which segregated out as 2 M : 2 m. A few exceptions from this expected ratio have been found and can be explained by the fact that 8-nucleate asci are occasionally formed which may produce only 4 spores, and it is a matter of chance which of the 8 nuclei a particular spore will contain. 5- and 6-spored asci showing deviations from the expected 2:2 ratio have been observed.

By spore crossings between two yeast types containing the same M-gene, hybrids have been obtained which yielded only maltose fermenting

spore progeny, since the hybrids were homozygotic with regard to the gene in question.

Overlapping of generations may easily lead to erroneous conclusions regarding the mode of inheritance.

The M genes are situated sufficiently far from the centromere to allow ca. 50 % crossing over between the genes and the centromere.

Linkage between the M-genes has not been observed.

These genes, each of which can induce fermentation, are situated either in separate chromosomes or are so far apart on the same chromosome that there is ca. 50 % crossing over between them.

By Röntgen irradiation of yeast types which were heterozygotic with regard to one M-gene, we have obtained ca. 1 % non-fermenting mutants. According to the appearance of their giant colonies, these non-fermenters, each arising from the same mother type, were identical.

True reverse mutation has not been observed, since e.g. we have not been able to produce the mutations represented by the series $M_1 \rightarrow m_1 \rightarrow M_1$. We have found, however, that recessive types are able to mutate to fermenting types.

R. BAUCH (Greifswald)

Die Konstanz der experimentell erzeugten Gigas-Rassen der Hefe

Im Jahre 1941 konnte erstmalig gezeigt werden, dass sich bei der Hefe durch Einwirkung bestimmter Chemikalien Rassen mit vergrößerten Zellen experimentell erzeugen lassen (1). Neben den anfangs verwendeten Stoffen vom

Typus der Mitosegifte wie Acenaphthen und Campher erwiesen sich später auch carcinogene Kohlenwasserstoffe wie Benzpyren und Methylcholanthren (3) und pflanzliche Wuchsstoffe wie Indol- und Naphthalinessigsäure (5) als gleichsinnig wirksam. Auch durch Radiumbestrahlung liessen sich Gigas-Rassen erzielen (7), während Colchicin bei der Hefe ebenso wie bei anderen Pilzen unwirksam war. Gigas-Rassen, die erneut mit den genannten Substanzen behandelt wurden, ergaben Stämme mit noch weiter vergrösserten Zellen, die Supergigas-Rassen (2). Gelegentlich kommt es auch zur Entstehung von Formen mit deutlich verkleinerten Zellen, die als Minor-Rassen bezeichnet wurden. Ein Teil der neuen Formen wurde nach vorherigen Kleinversuchen im Laboratorium in den praktischen Brauereibetrieb eingeführt. Die „Gigas-Biere“ zeichneten sich dabei gegenüber dem Ursprungsstamm durch besonders hervorragende Geschmacksqualitäten aus. Obwohl die Zytologie der neu gewonnenen Rassen nicht in wünschenswerter Weise geklärt werden konnte, wurde aus der weitgehenden Ähnlichkeit dieser Ergebnisse mit den in der experimentellen Genetik bekannten Polyploidisierungseffekten der Schluss gezogen, dass es sich bei den Gigas- und Supergigas-Rassen der Hefe um tetra-, bzw. octoploide Rassen handele (2). Zusammenfassende Darstellungen dieser Studien auf dem Gebiete der Chemogenetik wurden in den Jahren 1942 (4) und 1943 (6) gegeben.

Diese Untersuchungen wurden in der Folge von verschiedenen Forscherkreisen nachgeprüft, erweitert und bestätigt. Gigas-Rassen und andere Mutanten wurden bei der Hefe erzielt von SUBRAMANIAM (12, 17), SKOVSTED (18), LUTERAAN und DIENG (19) und MITRA und SUBRAMANIAM (20). Den gleichen Erfolg hatten THAYSEN und MORRIS (10) bei *Torulopsis utilis*. Bei verschiedenen *Penicillium*-Arten synthetisierten KOSTOFF (14) und SANSOME (15) Gigas-Stämme. Ein schwedischer Arbeitskreis um LEVAN interessierte sich besonders für die eigenartigen morphologischen Reaktionen, die Campher-Behandlung bei der Hefe auslöst. Bei Ein-

wirkung bestimmter Camphergaben wird das Sprossungswachstum der Hefe sistiert und an seine Stelle tritt ein mehr oder minder ausgeprägtes Mycelwachstum. LEVAN studierte, teilweise zusammen mit SANDWALL, diese „Campher-Reaktion“ der Hefe und erweiterte unsere Kenntnisse über den Wirkungsmechanismus des Camphers und ihm verwandter Stoffe erheblich (8, 11, 13, 16). Er konnte nachweisen, dass Campher auch an der Blütenpflanze (*Allium*-Test) als Mitosegift in Art des Colchicins wirkt (9). Seiner diffizilen zytologischen Technik gelang ferner der direkte Nachweis einer weitgehenden störenden Wirkung des Camphers auf die Kernteilung der Hefe. Damit konnte er die in unseren Versuchen nur postulierte Polyploidie der Gigas- und Supergigas-Rassen zytologisch belegen (16).

Die in den Jahren 1941 und 1942 synthetisierten neuen Heferassen wurden bis Anfang 1945 nach verschiedener Richtung hin experimentell überprüft. Für praktische Zwecke stand vor allem die Frage der Konstanz im Vordergrund des Interesses. Die Stämme waren in der Zwischenzeit laufend auf neue Nährböden übertragen worden und hatten also bei den letzten Prüfungen durchschnittlich ein Alter von 2-3 Jahren erreicht. Die Auswertungen geschahen nach den gleichen Gesichtspunkten und mit der gleichen variationsstatistischen Methodik, über die bereits im Jahre 1943 (6) berichtet war. Durch ausgedehnte Aussaaten auf Bierwürze-Agarplatten wurde überdies jeder Stamm auf seine Variabilität überprüft.

Bei dieser Analyse liess sich die Gesamtheit der Gigas- und Supergigas-Rassen in folgende Gruppen einteilen:

1. Stämme, die nach 2 Jahren sowohl im morphologischen Bilde wie bei den „Plattenanalysen“ völlig konstant ihre Gigasmerkmale behalten hatten.
2. Stämme, die zwar dem morphologischen und variationsstatistischen Bilde nach als reine Gigas-Formen anzusprechen waren, die aber bei den Plattenanalysen einige wenige Kolonien mit Zellen von normaler Grösse lieferten.
3. Stämme, die dem mikroskopischen Bilde

nach als normal gross zu bezeichnen waren, bei denen sich aber bei den Plattenanalysen mehr oder minder zahlreich Gigas-Typen herauszüchten liessen.

4. Stämme, die restlos wieder zur Normalgrösse zurückgekehrt waren und bei denen keinerlei Gigas-Formen mehr gefunden werden konnten.

Diese Ergebnisse werden dahin gedeutet, dass bei den verschiedenen Stämmen sehr verschiedene Grade der Ausbalanziertheit der Genome vorliegen. Völlig ausbalanziert sind nur die Stämme der Gruppe 1, bei denen keine Rückschläge zur Norm auftreten. Bei der Gruppe 2 ist die Vitalität der Gigas-Rasse genügend gross, um die seltenen abgespaltenen Normalzellen im Konkurrenzkampf innerhalb der Kultur nicht aufkommen zu lassen. Bei der Gruppe 3 dagegen vermehren sich die abgespaltenen Normalzellen bei der weiteren Führung so stark, dass sie die Gigas-Zellen zahlenmässig fast völlig überflügeln. Bei der Gruppe 4 schliesslich ist der Konkurrenzkampf innerhalb der Kultur zugunsten der Normalstämmen entschieden. Wir möchten daraus ferner den Schluss ziehen, dass unter den Gigas-Stämmen ebenso wie bei der der experimentellen Polyploidisierung der Blütenpflanzen sehr verschiedene Grade der Polyploidie, Subploidie und Hyperploidie vorliegen. Die konstanten Gigas-Stämme der Gruppe dürften als reine Polyploide anzusprechen sein.

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Discussion

Ö. WINGE: It has never been proved that the mutant types in yeast with large cells are real

polyploids, as nobody has counted the chromosomes or has been otherwise able to show that they were exactly triploids, tetraploids, etc. Personally I do not believe that they are. Several years ago I sent Professor BAUCH a typical haploid yeast culture, and Professor BAUCH attempted to make it diploid by means of a camphor treatment, but did not succeed. If he had succeeded the yeast would have been able to form spores. We must admit that we do not know much about the cytology of yeast.

A. SKOVSTED: The facts 1. that you are able to produce a giant type from a haploid, and 2. that this giant is to all appearance still a haploid with round cells (contrary to oval cells in the diploid), this argues against the assumption that the giants are polyploids.

Furthermore, the fact that you are able to produce the same giant type over and over again argues against the assumption that the phenomenon is due to chromosome disturbance. The facts available so far seem to favour an explanation on the basis of a general mutation, probably a directed one.

M. J. MATHIESON and D. G. CATCHESIDE
(Cambridge)

*Mutation in Bombardia lunata and
Chromocrea spinulosa*

The ascus in *Bombardia* is linear and ordered, the wild type ascospores being greenish grey. ZICKLER found two colour mutants, each distinguishable in the ascospores. In one, *rubiginosa*, the ascospores are pale reddish brown, in the other, *lactea*, they are colourless. The genes determining these characters are at different loci and are probably unlinked; *lactea* is epistatic to *rubiginosa*. Heterozygotes for either mutant gene show four wild type and four mutant ascospores in each one of the great majority of the asci. A minority, about 0.2 per cent, show either six wild type and two mutant ascospores or two wild type and six mutant ascospores. Tests, of stocks grown from the ascospores of aberrant *rubiginosa* asci, by means of crosses with wild type and mutant show that

the aberrant asci owe their origin to mutation at the locus in one of the four strands of the meiotic tetrad. No 5:3 or 3:5 asci were observed; very rarely there was an 8:0, but no 7:1 or 1:7. It is suggested that the mutation is induced in connection with cross-over breakage, but further investigation requires suitable markers in the neighbourhood of the locus for ascospore colour. No aberrant asci have been seen in a substantial number of homozygous wild type and mutant asci, so the phenomenon may be connected with heterozygosity at the locus concerned or may involve some complementary gene system as an activator.

The ascus in *Chromocrea* is also linear and ordered, each ascus regularly showing four large and four small two-celled ascospores. These are distributed according to the usual patterns typical of a single gene in tetrad segregation, with about 65 per cent second division segregation. Single large ascospores give cultures which produce a few stromata. These contain fertile perithecia which repeat the spore size segregation. Single small ascospores produce infertile cultures, lacking stromata. Mixed sowings are abundantly fertile; also the line of junction of large and small spore cultures is marked by numerous perithecia. In crosses of various morphological and colour mutants with the appropriate wild type (large or small ascospore), all perithecia developed along the line of junction show segregation for the morphological mutant as well as for ascospore size. Two of these mutants, brown exudate (*brx*) and fluffy (*fl*) show fairly close linkage with spore size. The results are compatible with the assumption that *Chromocrea* is heterothallic, the two mating type alleles also determining spore size. One allele, that governing large spores, occasionally mutates to the other allele. In this way, mating-type heterocaryons arise in cultures from single large ascospores and these form a moderate number of stromata and perithecia. The presence of both types of nuclei can be detected in hyphal tips dissected from isolated stromata.

The paper was read by D. G. CATCHESIDE.

Discussion

H. MARQUARDT: Can the abnormal segregation in *Bombardia* be interpreted by a rare occurrence of half-chromatid-chiasmata in meiosis? (Analogy to half-chromatid translocation.)

D. G. CATCHESIDE: This does not appear to account for mutation in each direction.

R. A. LEWIN: In view of the postulated occurrence of somatic mutations for mating-type and ascospore size in *C. spinulosa*, it might be expected that aberrant asci with spore-pair ratios of, say, 2 large to 6 small, would occur. Have any been observed?

D. G. CATCHESIDE: No, but they have not been sought especially. The size differences are not very great.

E. C. STAKMAN (St. Paul, Minn.)

Mutation and Hybridization in the Smut Fungi

Mutation and hybridization in the smut fungi vary greatly with species, most of which comprise many haploid biotypes differing in cultural characters, mutability, sexual combining ability and in factors for pathogenicity. Some species comprise thousands of haploid biotypes, many of which mutate abundantly and intercross freely.

Among twelve species of smuts studied at Minnesota, *Ustilago zeae*, *U. sphaerogena*, *Sorosporium syntherismae*, and *Sphacelotheca sorghi* were among the most mutable and *Ustilago kolleri* and *Ustilago avenae* among the least mutable.

Within *Ustilago zeae* and certain other species there are great differences in mutability of monosporidial haploid lines. Mutability is a heritable character, as shown by segregation for this character in mutable \times constant crosses and by increase and decrease in the degree of mutability of gametic progeny from mutable \times mutable and constant \times constant crosses, respectively.

Diploid monosporidial lines of *Ustilago zeae* have been obtained from crosses in which one

of the haploid lines has factors for autolysis of promycelia which is associated with a tendency to produce diploid sporidia. Diploid lines differ in degree of mutability.

The number of visible mutants in culture can be affected by physical and chemical agents. Uranium nitrate in culture media has greatly increased the number of visible mutants in mutable lines of *Ustilago zeae* and has stimulated mutation in otherwise constant lines.

Mutants may differ from parental lines in one or more of the following characters: mutability; general characters of colonies, such as size, topography, color and margin; sporidial or mycelial growth; size of sporidia; temperature relations; enzyme production; tolerance to toxic materials; sexuality; and pathogenicity.

Mutants are likely to deviate in a minus direction from parental lines, but occasionally they gain in one or more characters, including pathogenicity. There may be both loss and gain in the same mutant. Among 198 uranium-induced mutants of a haploid, monosporidial line of *Ustilago zeae* there were many combinations of plus and minus deviations for 13 cultural characters. Algebraic summation of the plus, minus and zero deviations for the 13 characters for each mutant showed that in 60 percent there had been neither a net loss nor gain, in 20 percent there was a net loss, and in 20 percent a net gain.

As a result of successive transfers to arsenic media monosporidial lines of *Ustilago zeae* have developed tolerance to concentrations five times the initial concentration. Adapted lines lost this ability after several cultural generations on arsenic-free media.

Variation due to recombinations between haploid lines within species is extensive in most smuts. In some species, such as *Ustilago zeae* and *Sphacelotheca sorghi*, there are many sex groups, but in others there appear to be only two. Certain monosporidial lines of *U. zeae* can unite to produce a strongly parasitic dicaryophase but not the true diplophase; chlamydospores are not produced.

In a single cross there may be all possible

segregation ratios among the sporidia produced on promycelia of different chlamydospores. For sex or cultural characters, for example, arrangement of sporidia on promycelia may be represented as follows: a, a, b, b; a, b, a, b; a, b, b, c; a, b, a, c; a, a, a, a; a, b, c, d or any other possible combination. In crosses between strict sporidial and strict mycelial lines of *Ustilago zeae* every possible combination of sporidia and hyphal branches appeared on promycelia, i.e. 4S:0M; 4M:0S; 3S:1M; 3M:1S; 2M:2S (S, S, M, M and S, M, S, M). There often is independent segregation for different characters.

There are an indefinite number of haploid biotypes within some species of smut fungi and new ones are continually arising as the result of mutation and recombination. Among the progeny of two monosporidial lines of *Ustilago zeae*, crossed about 20 years ago, more than 7500 biotypes have been produced by mutation and recombination. Nevertheless, no sexual combination has transcended the specific limits. *Sphacelotheca sorghi* and certain other species are probably almost as complex.

Certain interspecific crosses between *Tilletia* spp. of wheat, between the smuts of oats and between *Ustilago hordei* and *U. medians* resulted in recombination of several characters, including morphologic characters of chlamydospores and increased pathogenicity for certain varieties of wheat, oats, and barley, respectively. Extension of host range has resulted from certain other interspecific crosses also.

Several intergeneric crosses have been made. *Sphacelotheca sorghi* × *Sorosporium reilianum* is noteworthy because of the pronounced hybrid vigor of some combinations and the number of types of sori produced, including some that resembled those of *Tolyposporium filiferum*.

Discussion

A. A. BITANCOURT: At yesterday's meeting Dr. QUINTANILHA asked a Russian scientist how he could explain the results of tetrad analysis in *Coprinus* and other fungi which

consistently give a 2:2 segregation. LINDGREN gave several examples of 3:1 and 4:0 segregation in *Neurospora* and expressed the opinion that the 2:2 segregation might be the exception rather than the rule, the geneticists deliberately rejecting the mutants that did not conform to the Mendelian ratio. Inasmuch as Dr. STAKMAN also found lines of *Ustilago zeae* which did not show the 2:2 segregation, I would like to know his opinion on the matter.

E. C. STAKMAN: In *Ustilago zeae*, segregation ratios can vary with the cross. In this case the term "cross" is used to designate the combination of two monosporidial haploid lines. In many crosses a 2:2 ratio is exceptional. The ratios vary with the chlamydospore which produces the promycelium, where gametic segregation occurs. There can be all possible combinations of segregation ratios for a single character, and the ratios for another character may be different. As an example, in one cross made by the writer and his associates there were eight different combinations of segregation ratios for sex and cultural characters on promycelia from 11 chlamydospores.

In many crosses, between 20 and 60 monosporidial lines were obtained by isolating sporidia from promycelia of different chlamydospores; all lines differed in cultural characters, and none were identical with either parent.

One of the most convincing cases of segregation in all possible ratios is in the progeny from a cross between sporidial and mycelial lines of *U. zeae*. In this case the evidences of segregation are immediately visible, as some cells of the promycelium produce sporidia and others produce hyphal branches. The segregation ratios are as follows, with S indicating sporidia and M hyphal branches: 4S:0M; 4M:0S; 3S:1M; 3M:1S; 2M:2S. In the 2:2 segregation, the arrangement on the promycelia may be either S, S, M, M, or S, M, S, M.

It has been shown also that the number of cells in the promycelium of *U. zeae* varies greatly with the cross. In our experience with many crosses, the classical 4-celled promycelium does not always predominate.

R. A. LEWIN (New Haven, Conn.)
Genetics of Chlamydomonas moewusii
Gerloff

In order to study green plant metabolism by the methods of biochemical genetics, one would like to employ a heterothallic, unicellular alga with a rapid rate of division and a sexual cycle which can be controlled at every step. *Chlamydomonas moewusii* (complementary mating types of which were isolated by Dr. L. PROVASOLI in 1948) was accordingly selected for investigation with a view to its possible use as a genetic tool.

Active suspensions of *plus* and *minus* gametes can readily be obtained, and clumping and pairing take place when the mating-types are mixed. The clumps soon break up into pairs, in which the two partners, although morphologically identical, exhibit a marked difference in pairing behaviour. These pairs remain motile for some hours, the *plus* pushing the *minus* cell, and then gamete fusion takes place.

When zygotes are matured in continuous illumination, they develop thick walls and remain dormant indefinitely: however, a method of "dark starvation" has been evolved which may produce almost 100 % germination in 6-9 days. Following meiosis, 4, 8 or 16 swarmers are formed, the number depending on the period of initial illumination.

Single zygotes can be rapidly isolated on agar without special apparatus. On germination, the swarmers are allowed to disperse in a drop of water: as this dries, the cells are immobilised on the agar, where they give rise to separate colonies. These can then be picked and cultured for further examination, and in this way non-ordered tetrads may be analysed.

A number of mutants have been obtained by ultra-violet irradiation. These include:

1. ill-defined slow-growing or palmelloid types;
2. biochemical mutants, blocked in the photosynthetic mechanism, or in para-aminobenzoic acid or thiamine synthesis;
3. clones characterized by the formation of spherical, twinned or monstrous cells, or by the production of large volutin globules;
4. a number of strains in which the cells are unable to swim, either lacking flagella altogether, or possessing flagella which appear to be paralysed.

Nine of these mutants have been further studied genetically. The differences seem to be attributable to single genes, which behave in regular Mendelian fashion and segregate independently. There are significant indications of linkage between two pairs of characters. Since four distinct genotypes are frequently obtained from a single zygote, it is deduced that crossing-over, between locus and centromere, takes place as in other organisms in the 4-strand stage.

No deviations from regular heterothallism have been found: mating-type segregates regularly in a 2:2 manner. Mating-type (determined apparently by a specific flagella-agglutination factor) and mating-behaviour have not been observed to undergo recombination: it is therefore deduced that these are manifestations of closely-linked genes.

Additional interest is attached to this species, since it has been found (by PROVASOLI) to be interfertile with strains of *Chl. eugametos* Moewus.

SESSION 7

July 18th, 1—3 p. m.

Chairman: A. QUINTANILHA, Recorder: N. FRIES

SUBJECT:

Genetics and Cytology of Fungi

H. J. BRODIE (Bloomington, Ind.) *Sexuality, Inheritance Studies and Nuclear Migration in the Nidulariaceae (Gasteromycetes)*

Through the work of Dr. NILS FRIES and of the writer, the following species of the *Nidulariaceae* have been grown in single-spore culture: *Crucibulum vulgare* (FRIES, 1936); *Cyathus striatus* (FRIES, 1936); *C. stercoreus* (BRODIE, 1948); *C. vernicosus* (BRODIE, 1949); *Nidularia pisiformis* (FRIES, 1948); *Nidula candida* and *N. microcarpa* (BRODIE, 1950). All display tetrapolar or four-mating-type heterothallism.

Basidiospores germinate after being heated in a water suspension at 40°C for 48 hrs. Haploid mycelia are different morphologically from one another and from diploid mycelia as was shown by BRODIE for *Cyathus stercoreus*. Inheritance of mycelium color in this species appears to be determined by more than two pairs of factors.

Diploid mycelia of some species (e.g. *C. stercoreus*) fruited on various nutrient media to which some form of cellulose was added. Fruit-bodies produced on diploid mycelia representing combinations of different haploids were different morphologically, some being so unlike the parental wild type as to bear little resemblance to *C. stercoreus*, which explains the extreme variability of this species in nature.

In three respects, the *Nidulariaceae* display phenomena rare among *Basidiomycetes*.

1. Whereas, among most *Basidiomycetes* there exist large numbers of alleles of the sex factors,

FRIES showed that in *Crucibulum vulgare* and *Cyathus striatus* the number is limited, nine only being identified in *C. striatus*.

2. Monosporous mycelia are distributed unequally among the four sex groups, as has been observed by FRIES in *C. striatus* and by the writer in *C. stercoreus* and *C. vernicosus*. Probably a sub-lethal factor results in failure to obtain a representative selection of sex types among sporelings.

3. Whereas in many *Basidiomycetes*, during the process of diploidization, both mycelia of a compatible pair become fully diploidized, in *C. stercoreus* in certain pairings, only one haploid mycelium of a pair becomes diploid. This *unilateral diploidization* is being studied by Miss ISABEL FULTON, who has found that nuclear migration occurs only in combinations of mycelia possessing the B-b factors in common.

In all examples of unilateral diploidization, the haploid mycelium which behaved as acceptor of nuclei was shown by staining to possess two nuclei in each cell. Where this binucleate condition arose is unknown, but it can be produced artificially by combining two different haploids of the same mating type or two haploids of different mating type in which the pair of factors B-b is present, but only one of the pair A-a.

Discussion

B. P. MENZIES: With reference to the subject of the binucleate condition of haploid mycelia

in the species it may be of interest to note that in my study of the rust, *Puccinia suaveolens*, the haploid mycelia appear to be universally composed of binucleate cells.

A. GILLES (Louvain)

Evolution nucléaire chez Neurospora tetrasperma

Suivant la doctrine de CLAUSSEN, le cycle de développement des Ascomycètes comporte une dicaryophase s'amorçant dans l'archicarpe et se clôturant par la fusion dangeardienne dans l'asque jeune.

Chez *Neurospora tetrasperma* SHEAR & DODGE, il se forme des ascospores binucléées et « bisexuées », contenant chacune deux noyaux de polarité opposée. Si la doctrine clausсенienne est exacte, la spore, déjà dicaryotique, semble devoir donner naissance à un mycélium lui-même dicaryotique; la dicaryophase pourrait ainsi se vérifier dans l'ensemble du cycle.

Nous avons démontré précédemment que le mycélium de *Neurospora tetrasperma* n'est cependant pas dicaryotique, les noyaux n'y manifestant aucun appariement (P. MARTENS & A. GILLES, Le Botaniste, 1949, 34: 309).

Nos recherches ultérieures ont porté sur les conidies, l'archicarpe et les hyphes ascogènes.

Dans les conidies, le nombre de noyaux varie de 1 à 9. L'analyse de 136 conidies a révélé la répartition suivante: 26 cellules à 1 noyau, 32 à 2, 42 à 3, 11 à 4, 15 à 5, 2 à 6, 6 à 7, 2 à 9 noyaux. Les conidies à nombre impair de noyaux sont donc les plus nombreuses: 91 sur 136, soit 67 %. Cette répartition est analogue à celle observée dans les compartiments mycéliens et confirme, par conséquent, la valeur de nos conclusions pour cette première phase du cycle de développement.

Dans l'archicarpe spirale et peu cloisonné, les noyaux sont répartis d'une façon quelconque, sans constituer de groupes déterminés.

Dans les hyphes ascogènes, les numérations ont porté sur 103 compartiments, ce nombre excluant les cellules uni- ou binucléées apparte-

nant à un crochet ascogène, ainsi que les cellules binucléées résultant de la fusion de la pointe d'un crochet avec sa cellule basale. Ces 103 compartiments contiennent de 1 à 7 noyaux et se répartissent comme suit: 42 à 1 noyau, 30 à 2, 21 à 3, 6 à 4, 3 à 5, 1 à 7 noyaux. Ici encore, les compartiments à nombre impair de noyaux sont en majorité: 66 sur 103, soit 65 %.

Ces résultats correspondent à ceux auxquels l'exploration de plus de 1.000 compartiments d'hyphes nous avaient amené pour *Nectria flava* BON. (A. GILLES, La Cellule, 1947; 51: 369-400.) Ils obligent à écarter absolument, pour *Neurospora tetrasperma*, l'hypothèse d'une dicaryophase clausсенienne, tant pour le mycélium et les conidies que pour l'archicarpe et les hyphes ascogènes. L'état hétérocaryotique de l'ensemble des hyphes, impliquant un mélange de noyaux A et B, ne fait aucun doute; mais le dicaryon constitué dans l'ascospore doit se dissocier au cours de la germination et dès les premières mitoses, chacun des partenaires se divisant dès lors indépendamment. En outre, cette indépendance persiste au-delà de l'archicarpe, jusqu'à la formation des asques.

Le cycle de développement de *Neurospora tetrasperma* correspond donc, en fait, à celui que MARTENS (La Cellule, 1946, 50: 126-310) avait proposé comme vraisemblable en se basant sur le seul examen critique de la documentation fournie par les auteurs.

Discussion

P. MARTENS: L'amplitude des observations du Dr. GILLES et les résultats statistiques obtenus sur la répartition nucléaire dans le mycélium, les organes sexuels, les hyphes ascogènes, ne permettent pas d'échapper, semble-t-il, à la conclusion « anticlausсенienne » de l'auteur. Mais on doit relever la prédominance, assez extraordinaire, des compartiments à 3 noyaux (sommet de la courbe), tant sur ceux qui en ont moins (1-2) que sur ceux qui en ont plus (4-7). Cette constatation s'accorde parfaitement avec l'état hétérocaryotique — et non dicaryotique —

mais elle demande néanmoins une explication particulière. Il faut souhaiter que l'auteur nous l'apporte bientôt.

J. W. GROVES (Ottawa)

Sexuality and Heterothallism in the Sclerotiniaceae

In the *Sclerotiniaceae* three different types of sexual behaviour occur. 1. A single ascospore culture may bear both male and female sex organs and be self-fertile. 2. A single ascospore culture may bear both male and female sex organs and be self-sterile with compatibility determined by a single pair of allelomorphs. 3. Single ascospore cultures may be of two kinds that are sexually dimorphic.

Species of the first type are considered to be homothallic and self-fertile; those of the second type to be homothallic and self-sterile; and those of the third type to be heterothallic.

In heterothallic forms, self-fertilization is prevented by separating the sexes into two distinct thalli. In certain homothallic forms, although both male and female sex organs are present on the same thallus, self-fertilization is prevented by a mechanism of genetically controlled sterility factors.

Two mechanisms for bringing about outbreeding are present and confusion has arisen in the literature because both of these have been called heterothallism.

B. J. LUYET (St. Louis, Mo.)

Evidence and Lack of Evidence of Sexuality in Myxomycetes

The history of the development of our knowledge of the life cycles of *Myxomycetes* during the last 90 years (since DE BARY's monograph in 1860) can be divided into two periods: 1. Up to about the end of the last century, the investigators did not feel the need of assuming any sexual process to explain the sequence of stages that they had observed: flagellated swarmers, myxamoebae, microcysts, plasmo-

dia, sclerotia, spores; 2. From the beginning of the present century, they generally accepted the idea that the *Myxomycetes* reproduce sexually, not because they had discovered new facts which had to be accounted for by sexual processes, but because the idea was in the air. The first questions raised were not: What is the evidence for sexuality? but: Which elements are the gametes? Where does chromosomal reduction take place? Are the *Myxomycetes* homo- or heterothallic? For some forty years, then, there has been a parade of "opinions" about those questions. For example, claims have successively been made that the nuclei of the old plasmodia, before sporulation, fuse as gametes; that the nuclei of the young plasmodia do so; that gametic fusion occurs between myxamoebae, immediately before the formation of plasmodia; that it occurs earlier between flagellated swarmers. Several such claims, which show the light-heartedness with which the facts were handled, will be discussed.

Our own observations concern the contentions 1. that swarm cells occasionally seen tugging on a thin strand by which they are connected are in the process of gametic fusion, 2. that plasmodia will not develop, or at least that sporulation will not occur, in cultures originating from a single spore or a single swarmer which is not given the opportunity of mating. We found that the "tugging" swarm-cells, reported to fuse, repeatedly came together into one mass and separated again into two units joined by a thin strand, their behaviour being more that of twin-born elements trying to get loose one from the other than that of fusing gametes. (Observations made on *Comatricha pulchella*.)—Then, in a series of monospore cultures of *Physarella oblonga*, we obtained the complete cycle from single spores and from single amoebae resulting from any of forty successive divisions of a single swarm-cell liberated by a spore.

Thus many of the conclusions found in the literature on the existence of sexual processes in *Myxomycetes* are based on somewhat shallow factual evidence, and our own investigations

show that, in two particular cases, the observations were rather hastily interpreted as evidence of sexual behaviour.

The speaker concluded his report, in which several instances were mentioned of conclusions based on flimsy factual evidence, by asking the opinion of the audience on the desirability of forming a group of "matter of fact" biologists who wish to conduct an organized reaction against the tendency to proceed too light-heartedly in the observation of facts and to continue filling the shelves of the libraries with "confirmations" of accepted theories which usually account well for very poorly observed facts.

Discussion

P. MARTENS: Malgré le scepticisme partiellement justifié du Prof. LUYET, la convergence relative des résultats de plusieurs chercheurs non cités (SKUPIENSKI, WILSON, CADMAN, SCHÜNNEMANN, VON STOSCH, etc.), notamment quant aux numérations chromosomiques, nous porte à un stade, d'ailleurs variable, du cycle. D'autre part, les résultats négatifs obtenus par l'auteur pourraient peut-être s'expliquer par une sexualité « tardive », les fusions nucléaires sexuelles ne se réalisant que dans le plasmode adulte, ainsi que cela a été signalé chez certaines espèces (SKUPIENSKI).

B. J. LUYET: It was not possible in this short paper to enter into details on the results reported by the investigators mentioned by Prof. MARTENS. I refer the members of the audience interested in that subject to the study that I just published on it (*Biodynamica*, vol. 6, pp. 265-364, 1950). In that work I discussed three divergent views on the cycles of *Myxomycetes* held respectively by (1) SKUPIENSKI, (2) SCHÜNNEMANN, (3) WILSON & CADMAN, and VON STOSCH.

F. L. HOWARD: 1. In questioning previous observations of workers on sexuality in the *Myxomycetes* does the speaker know for certain that he had a uninucleate spore when he grew 40 generations of *Physarella* from a single spore?

2. How would the speaker account for cannibalism amongst myxamoebae?

B. J. LUYET: 1. May I point out first that my criticism of the views of other workers on the sexuality of *Myxomycetes* is not based on an opposition between their factual observations and mine. I claim that most of the proposed theories are badly in need of a solid foundation of observed facts and that my own observations are insufficient to permit any final conclusions on the type of sexual process prevalent in *Myxomycetes*, and even on the existence or inexistence of sex in them.

This point being clear, let me answer the question of the certitude of our observations on the nucleus. We have often observed myxamoebae with one nucleus visible *in vivo*; we never observed any with two. Occasionally the single nucleus of an amoeba slowly vanishes while the organism is under observation; that vanishing is followed by a cellular division and, after the division is completed, one nucleus can be seen again in each daughter cell. But this applies to the myxamoeba stage, we have no information on the nuclear content of the spores from which the amoebae originate or of the incipient plasmodium which the amoebae are to produce.

2. As to the question of cannibalism I will not attempt to "account for it" in this discussion of *sexuality*. I wish only to point to the possibility (or probability?) that cases of ingestion of one organism by another, or cases of mere coalescence, have been uncritically interpreted as cases of gametic fusion.

J. C. SOBELS: Miss SCHURE has published in "Antonie van Leeuwenhoek" 15, 1939, her work on *Physarum didermoides*. She observed reduction divisions before spore formation and she could follow the reduction of the number of the chromosomes and their partition among the spores. She counted the chromosomes, often the partition was irregular.

B. J. LUYET remarked that his suggestion of forming a group of "matter of fact" biologists had met with no answer.

SESSION 8

Jointly with Section FOB: July 19th, 9 a. m. — noon

Chairmen: R. HEIM and J. RAMSBOTTOM, Recorders: N. FRIES and E. BJÖRKMAN

SUBJECT:

Mycorrhiza and Related Subjects

E. MELIN (Uppsala)

Recent Studies on the Nature of Tree Mycorrhizae

During the last few years, experimental studies concerning tree-mycorrhizae and their components have been continued in my laboratory at Uppsala. The object of these studies has been to increase our knowledge of the nature of such mycorrhizae, the present paper dealing mainly with some of the recent results obtained.

In earlier investigations, my collaborators and I have shown experimentally that a very large number of fungus species form mycorrhizae with forest trees. In general, these fungi belong either to the Hymenomycetes or Gastromycetes.

Tree-mycorrhizal fungi studied are completely or partially heterotrophic with regard to thiamin when growing in a synthetic medium. Several species are favoured also by other B-vitamins, e.g. biotin or nicotinic acid.

Recent studies have shown that—at least in many cases—certain amino acids are also necessary for optimum growth of tree-mycorrhizal fungi in a synthetic medium containing ammonium salt as nitrogen source. A mixture of amino acids, given in the same proportions as in casein hydrolysate, produced in general a strong growth-stimulative effect. It was shown, however, that all necessary amino acids could be synthesized from ammonium nitrogen in a synthetic medium which contained the necessary vitamins. Several amino acids, however, could not be formed with sufficient rapidity to

produce optimum growth. The total effect of different amino acids may also be determined by the interaction between them as well as from the fact that certain amino acids, even in low concentrations, exercise a strong inhibitory effect. Different mycorrhizal fungi, however, reacted differently. For example, *Boletus variegatus*, *B. elegans* and *Lactarius deliciosus* were strongly stimulated by glutamic acid, whereas the same acid had little or no stimulative effect on *Lactarius rufus* and *Cortinarius glaucopus*.

Evidence is advanced that other, as yet unknown, growth factors are involved in the development of many tree-mycorrhizal fungi.

The vigorous development of the mycorrhizal fungi between the cortical cells of the short roots may indicate that pectins are readily utilized by the hyphae. Certain sugars are also good carbon and energy sources. So far as we know at present, cellulose is useless as a sole carbon source for obligate tree-mycorrhizal fungi in pure culture. However, recent investigations indicate that these fungi, under certain conditions, may produce cellulase which enables the hyphae to pass through the cell walls and invade the cells. On the other hand, BIRGITTA NORKRANS has shown that strong cellulose-decomposers, e.g. *Tricholoma fumosum*, can also form mycorrhizae with pine. According to this author, the difference in cellulase-forming ability between litter-decomposing and mycorrhiza-forming fungi may be a quantitative rather than qualitative one.

In studying the relationship between the components of tree-mycorrhizae, sterile root

cultures of pine have been used recently in my laboratory. If mycelium of a mycorrhizal fungus is introduced into a pure culture of a growing pine root, the short roots soon begin to branch dichotomously even before they have come into contact with the hyphae. The same effect could also be brought about by addition of a nutrient solution in which the fungus had been cultured. The dichotomous branching was therefore caused by exudates of the hyphae. It was shown by V. SLANKIS that auxins—e.g. β -indole acetic acid and α -naphthalene acetic acid—have the same influence on pine roots. Auxins also produced a rich development of short roots. The experiments indicate that in nature the intensity of the branching of tree mycorrhizae may depend on the rate of auxin production of their fungal components.

The formation of mycorrhizae means that hyphae of certain rhizosphere fungi invade the short roots. The infection therefore may be primarily a parasitic attack by the hyphae. Under natural conditions, however, tree-mycorrhizae represent—at least generally—a balanced parasitism in which the higher partner is also favoured. During the last few decades, facts have accumulated which show conclusively that most mycorrhizal fungi are beneficial or even necessary for the trees.

Experiments by A. B. HATCH showed that pine seedlings grown in prairie soil were much favoured in their growth by inoculation with mycorrhizal fungi. He also found that inoculated plants had a higher content of nitrogen, phosphorus and potassium than the control plants. By these experiments and others it has been confirmed that at least some mycorrhizal combinations are nutrient-absorbing structures. This conclusion is supported by some measurements recently made in my laboratory concerning transfer of radioactive phosphorus to pine seedlings by means of mycorrhizal hyphae. In these experiments, the leading principle was to arrange things in such a way that only the mycorrhizal hyphae would be exposed to the isotope. Cylindrical glass cups were placed at the bottom of wide-necked erlenmeyer flasks,

near the wall. Purified sand was put in the erlenmeyer flasks as well as in the cups, in amounts allowing the cup edges to be about 5 mm above the sand level. Nutrient solution was then added to both vessels in suitable quantities. After autoclaving, one aseptic seedling of pine was introduced in the outer vessel and somewhat later the cups were inoculated with *Boletus variegatus*. After a couple of weeks, the hyphae had grown over the cup edges into the sand of the erlenmeyer flasks and after two months mycorrhizae were very well-developed. The cultures were then ready for the treatment with P^{32} . The isotope was added to the cups in desired activities varying from 1 μ c to 1 mc in various experiments. After varied periods of exposure, ranging from a few hours to several days, the activities in different parts of the seedlings were measured with a Geiger-Müller counter. These measurements showed that the non-mycorrhizal tips of the main and the lateral roots contained only very small amounts of P^{32} , whereas segments bearing mycorrhizae contained considerable quantities of the isotope. Since the mycelia in the cups, when exposed to the radioactive solution, still had intact hyphal connections with the mycorrhizae, it seems evident that the radioactive component had been transported from its source to the mycorrhizae by the *Boletus* hyphae. The isotope had then been translocated to the main roots, stems and needles. Already after treatment for 7.5 hours with radioactive phosphorus, the isotope could be traced in the pine needles.

These experiments prove that mycorrhizal hyphae transfer nutrients to the tree roots. Much evidence suggests, however, that different species of mycorrhizal fungi are unequally effective in their contribution to the nourishment of the trees.

B. PEYRONEL (Torino)

L'étude des mycorhizes par l'observation directe

L'auteur de cette communication souligne l'intérêt que présente l'étude des mycorhizes

par l'observation directe, soit macroscopique *in situ*, soit microscopique sur le vivant en altérant le moins possible les liens mycéliens, souvent très délicats, qui mettent les mycorhizes en rapport avec le sol.

Cette étude ne doit pas être négligée si l'on veut donner aux recherches expérimentales une base rationnelle et solide et si l'on veut se former sur la symbiose mycorrhizienne une vision qui ne soit par trop incomplète et détachée de la réalité. Il illustre quelques-uns des résultats les plus saillants obtenus par cette méthode qui, quoique hérissée de difficultés, n'est pas plus sujette à erreur que la méthode expérimentale, appliquée dans un bon nombre de cas avec des succès éclatants à la synthèse mycorrhizienne. Il montre en particulier qu'il est possible, en bien des cas, en suivant une méthodologie et une technique appropriées, de découvrir et de prouver d'une manière tout-à-fait convaincante les rapports de symbiose existant entre plantes supérieures et champignons. Aucun des nombreux cas de rapports mycorrhiziques dénoncés par l'auteur, il y a déjà bien des années, n'a été démenti par les recherches successives faites en appliquant la méthode de synthèse artificielle, mais, au contraire, un bon nombre ont été confirmés. Un point important sur lequel se fonde cette méthodologie est la constatation qu'à chaque champignon producteur de mycorhizes correspond un type bien déterminé, spécifique, de celles-ci et que dans un bon nombre de cas il y a une étonnante analogie de structure entre la gaine mycélienne (mycochlène) des mycorhizes et le pied, parfois aussi le chapeau et même l'hyménium des champignons relatifs. Les vaisseaux lactificères des Russules et des Lactaires se rencontrent aussi dans les mycorhizes produites par ceux-ci et l'on peut y observer les mêmes réactions microchimiques qui distinguent les espèces âcres des espèces douces; les mycorhizes des espèces âcres ont aussi une saveur âcre nettement perceptible.

Contrairement à une opinion très générale, il semble bien que, dans un bon nombre de cas tout-au-moins, la gaine mycélienne n'exerce aucune fonction d'absorption et ne remplace

pas du tout les poils radicaux: c'est au mycélium qui envahit l'humus en y formant un réseau souvent très étendu qu'est dévolue la fonction d'absorber l'eau et les matières nutritives et de les convoyer vers les mycorhizes, tantôt moyennant de multiples filaments isolés qui pénètrent dans la mycochlène sur toute sa surface, tantôt par un petit nombre de cordons mycéliens plus ou moins différenciés.

Enfin, un résultat intéressant obtenu par l'A. dès 1940, est la constatation du rapport étroit qui existe entre l'intensité de l'illumination solaire et le degré d'infection mycorrhizienne chez certaines Fanérogames et chez deux Hépatiques (mycorhizes endotrophes).

En conclusion, la méthode de l'observation directe, en nature, et la méthode expérimentale se complètent réciproquement et c'est en les employant tour-à-tour qu'on pourra obtenir les meilleurs résultats dans l'étude si captivante, mais si difficile, de la symbiose mycorrhizienne.

Discussion

Le Prof. ROGER HEIM en remerciant le Prof. PEYRONEL de sa communication rappelle la part qu'il a prise dans la mise en évidence des relations mycorrhiziques par une méthode d'observation directe qui intéresse particulièrement les mycologues. Il insiste sur la parti que les systématiciens pourront tirer de telles remarques en précisant ou infirmant la valeur de groupes taxonomiques dont le comportement à ce sujet pourra être déterminé. Ainsi, tous les Bolets sont mycorrhiziques, mais les *Strobilomyces* qui, pour certains, sont, non pas des Bolets, mais des formes gastéroïdes, ne semblent pas mycorrhiziques: M. R. HEIM a pu s'en rendre compte, notamment dans les régions tropicales où les *Strobilomyces* sont saprophytes sur les bois. Enfin, il montre l'intérêt des observations de M. PEYRONEL en ce qui concerne le rôle de *Endogone* dont l'abondance dans certains sols, la nature si particulière, les variations dans la forme, souvent coralloïde, posent un problème que les nouvelles données de M. PEYRONEL pourraient éclairer, si elles se confirment.

H. VAN VLOTEN: 1. Même en Suède il y a des recherches très nettement faites dans la nature, dans les forêts, exécutées par exemple par M. le Professeur BJÖRKMAN et M. le Docteur MODÉSS. C'est cependant dans une direction un peu divergente que les vôtres. 2. Est-ce qu'il y a à votre opinion aussi avec les mycorrhizes endotrophes une influence nutritive aux plantes concernées?

B. PEYRONEL: Les mycorrhizes endotrophes à endophyte du type *Endogone* ou *phycomycète* ont certainement une part importante dans la nutrition de la plante qui en est pourvue. Cela résulte d'un côté du fait que, comme je l'ai montré dans mes travaux, le développement du champignon dans ces mycorrhizes n'est pas du tout limité à l'intérieur de l'écorce des racines, mais s'étend par de nombreux filaments au sol qui les entoure, ce qui porte à penser que l'endophyte, outre à modifier les propriétés osmotiques et enzymatiques des cellules infectées, puisse absorber directement du sol une partie au moins des principes nutritifs nécessaires à la plante symbiote. D'un autre côté, mes observations ont mis en évidence le fait que les filaments mycéliens de l'endophyte forment à la surface des racines mycorrhisées un réseau plus ou moins serré et passent aussi d'une racine à l'autre. Dans certains cas je crois avoir observé le passage du mycélium des racines d'une espèce déterminée à celles d'une espèce différente. Ce fait, mis en rapport avec celui qu'une même espèce d'*Endogone* peut produire des mycorrhizes sur plusieurs espèces de plantes supérieures, m'a porté à énoncer, dans un travail publié en 1937, l'hypothèse que les éléments qui constituent une formation végétale puissent former un tout organique, dans lequel les éléments mêmes seraient étroitement liés entre eux par des rapports nutritifs complexes et variables, grâce aux champignons mycorrhizogènes. Par l'intermédiaire de ceux-ci certaines Fanérogames pourraient soustraire des substances nutritives à d'autres, ou bien en céder, se comporter comme des parasites ou bien être à leur tour parasites.

Je reconnais volontiers que cette hypothèse

est bien hardie et qu'elle demande une plus large base d'observations.

G. NOACHOVITCH: L'opinion que M. le Prof. PEYRONEL vient de formuler relativement au passage vraisemblable de filaments mycéliens d'une espèce hôte à une autre, de racine à racine, me paraît devoir être rapproché des assertions de JACOB DE CARDEMOY, déjà anciennes, conformément auxquelles des filaments mycéliens passeraient, dans certains cas, des plantes-supports du vanillier, orchidée épiphyte, dans les racines de cette dernière plante, la plaçant dans un état pathologique. Le même auteur a, de même, affirmé avoir constaté de tels transferts de filaments mycéliens des plantes-supports du poivrier aux racines de celui-ci. L'étude approfondie de ces rapports présente un intérêt économique évident.

R. HEIM demandait des renseignements sur les cystides qu'on observe sur les mycorrhizes (ectotrophes) produites par les Russules (*Russula*).

B. PEYRONEL: Les cystides dont j'ai parlé sont celles qui sont en rapport avec les vaisseaux lactifères et qui, comme ces derniers, présentent des réactions caractéristiques avec certaines substances, telles que, par exemple, la teinture de gaiac ou la sulfo-vanilline. Dans les mycorrhizes produits par les Lactaires (*Lactarius*) j'ai le plus souvent observé une mycochlène (revêtement mycélien, gaine mycélienne) lisse, sans poils ni cystides, mais toujours coexistant avec des vaisseaux lactifères.

D. T. MACDOUGAL and J. DUFRÉNOY
(San Francisco, Calif.)

*Mycorrhizae of Excised Roots of the
Monterey Pine, Pinus radiata*

The "Monterey Pine" grows spontaneously in a restricted area of the Monterey Peninsula on the Pacific Coast, in California.

Rootlets which have been severed from the parent tree, but allowed to remain in the forest litter, retain their connection with the fungi entering into the mycorrhizal relationship, and

continue to live and grow for indefinite time; the terminal meristem is the site of caryokinetic processes, and forms new cells, some of which differentiate into the normal vascular system (phloem and xylem) pericycle, endodermis, and cortical parenchyma. The cortical parenchyma progressively becomes infiltrated with the hyphae of ecto-endotrophic mycorrhiza components; the vascular tissue, ensheathed within the layers of pericycle and endodermis cells (each containing vacuoles full of tannin-rich vacuolar solution) remains free of mycelial infiltration.

The excized rootlets, cut off from the photosynthetic part of the parent tree, none the less differentiate some mitochondria into amyloplasts, wherein starch is being stored; other mitochondria, notably in the phloem parenchyma, differentiate into proteoplasts, wherein protein material is stored.

Cytological evidence is thus offered that rootlets, free from the parent tree, not only satisfy their carbon and nitrogen metabolic requirements for continued growth, but even store surplus carbohydrates and proteins.

The paper was read by L. E. WEHMEYER.

E. BJÖRKMAN (Stockholm)

A New Theory for the Formation of Ectotrophic Mycorrhiza

Since mycorrhizal fungi are apparently present in most forest soils and soils which have carried trees in the not too distant past, the mycorrhiza problem as far as forestry is concerned may be divided into two parts: 1. the physiological significance of the mycorrhizal association for the tree and the fungus, 2. conditions necessary for the formation of mycorrhizae. As many observations have shown the symbiotic relationship may, at least in certain circumstances, benefit the trees as well as the fungi, the actual conditions under which the symbiosis is established will be discussed. This problem, which from the point of view of forestry is of first importance, provided that the

importance of mycorrhizae to the tree is recognized at all, has received only incomplete attention from the ecological point of view in the abundant literature on mycorrhizae (cf. BJÖRKMAN 1949, Sv. Bot. Tidskr. 43). Very few investigations have enquired into the manner in which the several factors, active in natural environments, influence the formation of mycorrhizae. Results from laboratory experiments carried out under very special conditions are only of value if they can be fitted into wider ecological relationships and are interpreted from the point of view of the biology of the tree as well as of the fungus.

With a view to confirming HATCH's (1937) results under Swedish conditions, and also studying the conditions necessary for the formation of mycorrhizae from the point of view of the fungal symbiont, the author carried out a series of greenhouse and laboratory experiments in 1937-1942 using different forest soils and also nutrient solutions in glass flasks under sterile conditions; at the same time the development of mycorrhizae in various types of forests in different parts of Sweden was studied. The results of these investigations, published in 1942 (Symb. Bot. Ups. 6: 2), gave rise to a new theory of the development of mycorrhizae in pine and spruce which enabled the apparently contradictory results obtained from the use of nitrogen, phosphorus, potassium and calcium fertilizers, and from the shading of seedlings, to be explained.

The results obtained demonstrate that mycorrhizae develop best in strong light, in all cases more than 25 % of full daylight, and at a certain, but not too great, deficiency of easily available nitrogen or phosphorus. Mycorrhizae develop characteristically if the roots of the host plant contain a surplus of soluble carbohydrates. The importance of growth-promoting substances for the formation of mycorrhizae was discussed.

The new theory is also fundamentally in agreement with recent discoveries concerning the formation of nodules in leguminous plants, and also in the alder.

SESSION 9

July 19th, 1—4 p. m.

Chairman: W. H. SCHOPFER, Recorder: N. FRIES

SUBJECT:

Physiological Aspects on the Production and Action of Antibiotics

SELMAN A. WAKSMAN

(New Brunswick, N. J.)

Antibiotics and their Significance in the Physiology of Microorganisms

The Antibiotic Concept

It has long been recognized that certain groups of microorganisms have the capacity to antagonize or inhibit the growth of other organisms. Various theories have been proposed to explain this effect. Some of these were based upon the concept of competition for space or for nutrients among microorganisms; others were based upon changes in the composition of the medium produced as a result of growth of the organisms, such as exhaustion of nutrient substances, changes in reaction of medium due to formation of acids or alkalies, reduction in oxygen supply, or creation of other conditions which have an unfavorable effect upon the organism. It has gradually become recognized, however, that one of the major factors, if not the most important one, responsible for growth inhibition of one organism by another is its ability to produce specific chemical substances, now known as antibiotics.

This idea that antibiosis is due to the formation of certain growth-inhibiting compounds which have the capacity to function in a manner similar to that of the living organism itself is of but recent origin. It has now completely replaced the rather vague ideas that once prevailed concerning the "staling" of the medium as a result of the growth of certain organisms and the confusion that existed formerly between the concepts of parasitism and pathogenicity of microorganisms, on the one hand, and antibiosis, on the other.

The ability of various microorganisms to produce antibiotic substances is both qualitative and quantitative in nature, comprising differences in the nature of the antibiotic and in its concentration. These variations depend upon the nature of the organism producing the antibiotic, the composition of medium in which the organism is growing, and conditions of growth, such as aeration, temperature and reaction.

The property of forming antibiotics is not a group characteristic but, rather, is typical of a given strain of organism. Thus, out of numerous strains of *Streptomyces griseus* that may be isolated from soils, river muds, composts and peats, only very few are able to produce streptomycin, others form grisein, still others give rise to various still unidentified antibiotic substances; a large number of the strains are unable to produce any antibiotics at all, at least under the particular conditions of culture.

Many of the antibiotic-forming organisms will give rise to mutants, under the influence of various conditions of growth and nutrition, and especially as a result of specific irradiations. These mutants may show a completely changed picture so far as their antibiotic-producing capacity is concerned. Thus, a culture of *S. griseus*, first isolated in our laboratory in 1915 and grown for more than 30 years on synthetic media, failed to form any streptomycin when tested recently. Upon irradiation, however, this culture gave rise to a number of mutants, one of which was able to produce streptomycin. The same culture was deposited in the Baarn Collection in 1920, where it has been grown during these years on organic media. When recently obtained from that Collection and tested, it was found to produce an antibiotic

substance, which was different, however, from streptomycin. The streptomycin-producing strains isolated in 1943 also yielded variants or mutants, under cultural conditions alone; some of these either failed to form any antibiotic or produced a pigmented type of antibiotic which was distinctly different from streptomycin. It was also possible to obtain a variety of mutant strains by means of irradiation of the culture; some of these gave much higher yields of the antibiotic than the mother culture.

One of the major properties of an antibiotic is its selective action upon different groups of microorganisms, or its antibiotic spectrum. Some antibiotics, like gramicidin and penicillin, are largely active against gram-positive bacteria; others, like polymyxin, are active largely upon gram-negative bacteria; still others, like streptomycin and neomycin, are active upon certain bacteria within each group. Some, like streptothricin, are also active upon fungi; others are active only upon fungi and not upon bacteria. Some, like aureomycin and chloramphenicol, act upon rickettsiae and the larger viruses; others, like streptocin, act upon trichomonads; still others, like borrelidin, act upon *Borrelia* or various protozoa. Some antibiotics are specifically active only upon certain limited groups of bacteria, like *Mycobacterium tuberculosis*, and not upon others.

The spectral variations of the antibiotics, both qualitative and quantitative, are usually of two types. First, there is the natural variation among species within a certain group: the concentration of the antibiotic required to inhibit the growth of one species will vary from that of another; even some strains within a given species may show greater sensitivity or resistance than other strains. Second, there is the individual cell variation: in a given population of *Escherichia coli*, the great majority of cells are sensitive to 1 or 2 units of streptomycin per milliliter of culture; about 100 to 200 cells out of 200 000 000 may be resistant to 4 units; a few cells, 5 to 10, may be resistant to 10 or 12 units of streptomycin per milliliter of culture. This variation explains the develop-

ment of graded resistance to this antibiotic by various cultures of bacteria.

The antibiotic concept thus comprises a highly complex group of relations between organisms producing antibiotics and organisms sensitive to them. The significance of antibiotics in the growth of microorganisms, especially their effect upon other organisms in a mixed population; the importance of antibiotics in natural processes; the utilization of antibiotics as chemotherapeutic agents for the control of human and animal diseases; and their potentialities in the control of various plant diseases are far-reaching.

Antibiotics and Survival of Microorganisms

The tremendous panorama that has been unfolded as a result of the rapidly increasing knowledge of the production of antibiotics by microorganisms has tempted many investigators to speculate upon the significance of these products in the survival of antibiotic-producing organisms in a natural environment. The theoretical and practical considerations for such speculations are based upon certain popular concepts that have their roots in the field of folklore, often even in mythology, and in certain popular observations, some of which have led to practical applications. It is sufficient to cite the following facts:

1. Mixed infections have often been found to be milder than pure infections. This observation was frequently used as the basis for control of certain serious diseases, like anthrax or tuberculosis, by the application of less pathogenic or saprophytic organisms.

2. Certain practices of surgery are based upon the creation of conditions favorable to the development of antagonistic microorganisms. During the Spanish Civil War, the method of cast surgery or plaster treatment of wounds was used extensively; the saprophytic bacterial flora prevented infection of the wounds. The only objectionable part of this method of treatment was the putrefactive smells that such wounds produced.

3. The rapid destruction of various patho-

gens that find their way into the soil must have been noted in ancient times. This was fully confirmed through detailed bacteriological studies of the soil. Certain soils have been frequently spoken of as "immune" to specific pathogens, such as "cholera-immune soils."

4. When polluted water contains cells of the pyocyanus organism, the typhoid bacillus never has a chance to develop, or at least will not show its presence in the water, as determined by the presumptive tests.

5. The replacement of one bacterial flora by another in the intestinal canal, either by special methods of nutrition or by consumption of bacterial cells, offers another illustration of the antagonistic effect of microorganisms. Although this concept, originated under the auspices of МЕРЧНИКОВ, contributed little to our knowledge of antibiotics, it has tended to clarify somewhat the idea of existing bacterial populations. *Escherichia coli* has been used for replacing pathogenic bacteria in the gut. In the treatment of diphtheria organisms recourse was had to the use of lactic acid bacteria and *Staphylococcus aureus*; the resulting effects were not always favorable, however, to the host. The administration of various yeasts also had a certain popularity at one time, with uncertain results. Cultures of lactobacilli were used for both internal and external administration, as in the treatment of vaginal trichomoniasis. Cultures of *Lactobacillus acidophilus* are said to be beneficial in the treatment of various forms of diarrhea and dysentery.

6. Numerous efforts to replace a given population in the soil by another artificially introduced there led to rather discouraging results, unless accompanied simultaneously by a change in soil management, as by liming of the soil, addition of stable manures, or by growing leguminous or other host plants.

These facts as well as numerous popular observations, which need not be considered here in detail, have given rise to certain speculations, some of which may well be given further consideration.

Struggle for existence. There was a time when

the concept of "antibiosis" was almost synonymous with that of "struggle for existence." No wonder, therefore, that the ability of a given organism to produce an antibiotic was considered "purposeful" in nature, in order for the organism to protect itself against attack by other organisms. Detailed analysis of the known facts, however, hardly supports such speculation. The production of penicillin and streptomycin by the respective organisms offers excellent illustrations in this respect.

Penicillin is produced by certain fungi growing in pure culture, in highly selective media, which are rich in glucose, corn steep liquor, and other materials. The soil, in which live most of the aspergilli and penicillia capable of producing penicillin, presents no such nutritive medium for the formation and accumulation of this antibiotic. Under the best of conditions, only traces of penicillin could be formed in the soil, because of the limitation of the food supply. Since penicillin is readily destroyed by various bacteria that are abundant in the soil, this antibiotic, even if produced in traces, would be very rapidly destroyed by these bacteria, which form penicillinase. Most important of all, penicillin is not effective against fungi and most of the gram-negative bacteria; both of these groups of organisms comprise a large proportion of the soil population, and it is with these that the penicillin-forming penicillia and aspergilli would have to compete for nutrients. Of what importance can penicillin, therefore, be to the organism producing it in its struggle for existence in the complex soil population?

Streptomycin presents a somewhat different problem or even group of problems. 1. This antibiotic is highly stable and is not destroyed readily by other organisms. 2. For the production of streptomycin, a protein-rich medium is required. 3. Even if only a few cells of bacteria find their way into a big tank where *S. griseus* is growing, such bacteria multiply so rapidly as to prevent streptomycin formation. 4. What could be expected to occur in the soil where only very few cells of *S. griseus* are present, as compared to the vast microbio-

logical population; when still fewer of these cells are able to produce streptomycin; and when the soil contains only a limited number of nutrients required for streptomycin production? 5. Streptomycin is not effective against fungi, with which *S. griseus* would have to compete. 6. Finally, all the bacteria and actinomycetes that are sensitive to streptomycin can readily adapt themselves to it; hence, even if streptomycin were produced in the soil, its microbiological population would have long ago adapted itself to the antibiotic, thus rendering it completely ineffective. Of what potential importance can this agent be, therefore, to the organism producing it in its struggle for existence?

Similar processes of reasoning can apply to most of the other antibiotic-producing organisms. If an antibiotic would be of any help to the organism, one would expect that the soil would be largely inhabited by antibiotic-producing organisms. This is actually not the case.

Antibiotics for obtaining food. Microorganisms produce a variety of mechanisms, which are mostly enzymatic in nature and which enable them to obtain and to utilize the available nutrients, or to transform them from unavailable into available forms. This phenomenon is so pronounced among microorganisms that the ability to produce a given enzyme can be stimulated greatly by the presence in the culture of a specific substance upon which the enzyme has the capacity to act. It is even believed that organisms may develop the property of producing a certain enzyme, which it did not possess previously, merely upon contact with the particular substance. Under the influence of these considerations, DUBOS proceeded to enrich a soil with a variety of living bacteria, to encourage the development of organisms which would have the capacity to destroy such bacteria. By this procedure, he succeeded in isolating *Bacillus brevis*, an antibiotic-producing organism. A careful consideration, however, of the processes involved in these experiments will bring out the fact that the isolation of *B. brevis* following enrichment procedures was a

mere coincidence. The above process of reasoning would have been logical if antibiotics were mere enzymatic mechanisms which the organism uses for obtaining food. This is not the case: the action of antibiotics upon bacteria consists in interfering with certain reactions of growth, multiplication and respiration that are apparently, in most instances, distinct from the hydrolytic and lytic mechanisms required for the nutrition of the organisms. The killing of bacteria by antibiotics or the interference with their growth does not serve the purpose of supplying food to the organisms producing the antibiotics. The latter property is merely accidental. There is no purposefulness in this reaction.

Antibiotics and the gastrointestinal bacterial population. The bacterial population of the gastrointestinal canal offers an excellent illustration for postulating the role of the antibiotic-producing organisms in favoring their survival and multiplication in a mixed population. Such postulation can be based upon the ability of various strains of *E. coli* to form an antibiotic, or rather a group of antibiotics, known as colicines. These have a highly selective effect upon other strains of *E. coli*, as well as upon certain other organisms present in the intestinal population, such as *Shigella* species. The antibiotic spectrum of the colicines is very narrow and is characterized by a high degree of selective action upon other bacteria. This suggests a possible explanation for the presence of particular species of bacteria in a gastrointestinal population. Unfortunately, the factual data do not appear to substantiate the existence of single strains of *E. coli* in such a population, based merely upon their antibiotic-producing capacities. In their competition with the lactic-acid bacteria, for example, provided an available sugar is present, the colon group does not come out the victor. Thus a group of antibiotic-forming organisms fails in competition with a group of non-antibiotic-forming organisms.

Antibiotics and the soil population. The great complexity of the soil microbiological population and the capacity of many of its members

to form antibiotics hardly justify the assumption that this property plays an important role in determining the nature of the population. Admittedly, when foreign organisms are introduced, be they animal pathogens, like *Bacillus anthracis*, *Corynebacterium diphtheriae* or *Eberthella typhosa*, be they beneficial bacteria, like *Rhizobium leguminosarum* that produce nodules on the roots of leguminous plants, or be they bacteria and nematodes capable of destroying injurious insects, like the larvae of the Japanese beetles—they will not survive long in the soil. They may survive, of course, when a host is present, as when the legume plant, which can protect such bacteria or give them a temporary or permanent habitat, is growing in the soil. The destruction of the introduced organisms may be due to a lack of suitable food or conditions for their development, or it may be a result of the antibiotic effect of the soil population. This is not a result of specific stimuli from outside, but of existing properties of antibiotic-producing organisms inhabiting the soil.

Formation of Antibiotics

The nature of the antibiotic produced in a given medium and its concentration are influenced, if not controlled, by the composition of the medium in which the organism is growing and by the environmental factors or conditions of growth. Thus, one type of penicillin may be formed by certain strains of fungi under one set of conditions, and another type of penicillin by other strains and under other conditions. Since many antibiotic-producing organisms are able to form more than one antibiotic, the relative concentration of these is also greatly influenced by the changing conditions of culture.

Media and environment. Selection of the medium for growth of the organism and formation of the antibiotic is highly important. In some cases, synthetic media are used; others require complex organic media. Frequently, the presence of particular precursors is required, before certain antibiotics, such as the penicil-

lins, can be produced in large concentrations. One medium may be used for spore germination, another for massive growth of the organism, and occasionally still another for production of the antibiotic. The nutrients present in the medium are required for growth, as precursors for the particular antibiotic, and for buffering purposes to prevent unfavorable changes in the composition of the medium, such as acidity and alkalinity.

Our knowledge of the mechanism of antibiotic formation by various organisms is still very incomplete. Certain antibiotics, such as the polypeptides, are derived from the cell constituents, since they are isolated from the cell material or from its autolytic products. Other antibiotics, as penicillin, are favored by the presence in the medium of certain compounds which contain the constituent groups of the penicillin molecule.

Among the environmental factors that influence the production of antibiotics, aeration, temperature and reaction are most important. So far as we know at present, antibiotics are produced only by aerobic microorganisms or by organisms living in an aerobic environment. This is the reason why either shallow layers of medium are used in stationary cultures, or forced aeration of medium is employed in deep cultures. The extent of aeration frequently controls the success of a given process, different organisms varying greatly in this respect. The temperature range for optimum production of antibiotics lies between 20° and 35° C: above and below this range, growth of an organism will occur with only limited, if any, production of the antibiotic. Frequently optimum growth temperature does not correspond with optimum antibiotic production. The reaction effect differs for each antibiotic; since penicillin is an acid and streptomycin a base, one must logically expect an acid reaction of the medium to favor the first and an alkaline reaction the second. Addition of glucose to the medium may serve as a source of energy for the growth of the organism, or of acid favoring production of the antibiotic. In the case of basic antibiotics, the

acid produced must first be destroyed before antibiotic formation takes place.

Antagonistic microorganisms. The ability to form different antibiotics is not limited to a single organism or to a group of organisms. Penicillin can be produced by various strains of *Penicillium notatum*, *P. chrysogenum*, *P. crustaceum*, *Aspergillus flavus*, and a variety of other fungi. Four distinct types of variation are involved in this connection: a) strain variation of the penicillin-producing organism; b) type of penicillin produced by the various organisms; c) quantitative variation in production of penicillin with different strains and different media; d) formation of antibiotics other than penicillin by different organisms under different conditions.

These factors must be considered in any selection of strains or in any improvement of cultures for penicillin production. The development of suitable media, the selection of proper conditions for growth, the development of test procedures, the methods used for isolation of the penicillin from the culture—will all depend upon the above variations.

In the selection of new strains, advantage is taken of the natural variations among the various freshly isolated cultures and of the effects of irradiation upon the formation of new mutants. This involves the testing or screening of many thousands of cultures. The isolation of new penicillin-producing strains, favored by the above procedures, is now history. The yield of penicillin in the culture has been increased from 1 or 2 units per milliliter to a thousand or more units. The same is true, to a somewhat less spectacular extent, of streptomycin. When a culture of *S. griseus* is plated out on a synthetic or on an organic medium and the various colonies are picked and tested for their antibiotic-producing capacity, the following variations will be obtained: a) A few colonies produce a high concentration of streptomycin; these yield the most desirable strains for the production of this antibiotic. b) A number of colonies produce limited concentrations of streptomycin, ranging from mere traces to fairly

good yields. c) A few colonies, especially those that do not form the characteristic aerial mycelium, have lost the capacity to produce streptomycin; this capacity can be regained under suitable conditions of culture. d) Some colonies may have developed a new capacity to produce other types of antibiotics. It can, therefore, truthfully be said that one is dealing here with a living system, and if there is anything "constant" about such a system it is its variability, or, may I say, its "inconstancy".

Destruction, Inactivation and Adsorption of Antibiotics

Numerous mechanisms are known which tend to reduce the antibacterial activities of antibiotics. Different antibiotics vary greatly in this respect: some are completely destroyed, others are reduced in their potency, still others are temporarily inactivated or brought to a state in which their activity is manifested not at all or only under certain conditions.

Enzymatic agents. Next to the chemical reagents which destroy antibiotics under conditions that are usually too extreme to compare with those existing in living systems, enzymes occupy a prominent place among the antibiotic-destroying mechanism. Penicillin is completely destroyed by penicillinase, an enzyme which is formed by a variety of bacteria and fungi. Chloramphenicol is also said to be destroyed by an enzyme designated as "chloromycetinase." Occasional references are found in the literature to an enzyme, streptomycinase, which is said to destroy the corresponding antibiotic; in most cases, this was shown to be a phenomenon of inactivation rather than of destruction.

Inactivating mechanisms. Among antibiotic-inactivating mechanisms, that of streptomycin comes first to mind. A number of agents, many of which possess reducing properties, are capable of inactivating this antibiotic. It is sufficient to mention cysteine, hydroxylamine, and thioglycolic acid. The antibiotic potency of streptomycin is not destroyed by these agents, since its activity can be restored by removal of the inactivating agent. This is true, for example,

of cysteine when it is oxidized with iodine. Some antibiotics are greatly affected in their potency by a change in reaction of the medium. Streptomycin, neomycin and other basic antibiotics are greatly favored by an alkaline reaction, their maximum potency being at pH 8.2 or 8.4. With a decrease in alkalinity, the potency is reduced, so that at pH 6.0 or 6.2, their activity is only one half or less than at the optimum. At still greater acidity, the substances may be completely inactivated, although they are not destroyed.

Among the most important inactivating mechanisms, from a chemotherapeutic point of view, are those exerted upon the activity of antibiotics by the blood system. In some of the earliest studies of the tyrothricin complex, it was demonstrated that some of its constituents, notably gramicidin, are not active in the blood. Chetomin is also completely inactivated by the blood.

Adsorption of antibiotics. Various antibiotics can be adsorbed on certain surfaces, as in the case of the soil. This does not necessarily indicate that their activity is thereby destroyed. Here as well, different antibiotics vary greatly. The basic ones are adsorbed more readily into the base exchange complex, whereby the acid ones may remain more active.

Mode of Action of Antibiotics

Among the problems dealing with the physiological significance of antibiotics, none is of greater significance than their mode of action upon bacteria. The ability of an antibiotic to destroy bacterial cells or to inhibit their growth, and especially the fact that this takes place in the tissues of the host without affecting the cells of the host itself, present a phenomenon of the highest importance in chemotherapy. This is intimately associated with the selective action of antibiotics upon different cells, whereby one cell is affected and not another. This selective action extends beyond that involving microbial cells, to cells of higher forms of life as well.

The real solution of this problem is to be

looked for in the nutrition, growth, and multiplication of the cells. Different antibiotics affect different mechanisms; this is responsible for the fact that an organism resistant to one antibiotic may remain sensitive to another. The overlapping sensitivity of different antibiotics points to a similar mode of action upon bacterial cells. The extreme toxicity of certain antibiotics to animal tissues points either to a lack of differentiation or selective action of the agent upon the bacteria and upon the host cells, or to different mechanisms possessed by the same antibiotic agent.

Certain pertinent data on the antibacterial action of streptomycin have been discovered which make possible the presentation of a tentative theory to explain its mode of action upon bacteria. In the synthesis of its cell material, the bacterial cell carries through certain intermediary metabolic reactions, some of which are interfered with by the presence of a certain number of streptomycin molecules. The organism unable to synthesize new cell substance automatically dies. A few cells in the bacterial culture may possess another metabolic mechanism which enables them to synthesize their cell substance and which is not interfered with by streptomycin. When the cells possessing the primary mechanism die off, only those that possess the secondary mechanism are able to survive and give rise to a bacterial population or culture which is resistant to the effect of streptomycin.

The above theory explains the selective action of streptomycin upon different bacteria, upon bacteria vs. host cells, as well as the development of resistance. The formation of new strains which are dependent upon streptomycin for their growth can also be postulated by this theory. The only assumption necessary is that in killing off the sensitive cells and enabling the few cells that possess an alternate metabolic pattern to survive, streptomycin enters into one of the intermediary metabolic products of some of these cells, which thus become dependent upon its presence for their growth.

A better understanding of the mode of action

of antibiotics will make possible the synthesis of new chemical compounds which have similar properties and which are less toxic and easier to handle.

The field of antibiotics has contributed to a better understanding of the physiology of microorganisms, their role in mixed natural populations, and their utilization in the treatment of infectious diseases. It has opened new vistas for the microbiologist, the chemist, the clinician, the veterinarian and the plant pathologist, and especially it has pointed the way to a better understanding of the survival of microorganisms in nature and their complex physiological reactions.

H. TAMIYA (Tokyo)

Some New Approaches to the Problem of Mode of Action of Antibacterial Substances

The influence of various antibacterial substances upon the course of the logarithmic growth curve of bacteria was investigated systematically using mainly *Staphylococcus aureus* and *Escherichia coli* as test organisms. A comparative survey of more than 90 substances of different chemical categories showed that in respect to the modifications brought about in the three phases of bacterial growth (the lag, logarithmic and stationary phases), there can be distinguished four main types of inhibition, viz, 1. the inhibition causing only the prolongation of the lag phase without modification of the logarithmic and stationary phases (various mercury compounds, quinones, etc.), 2. suppression of the logarithmic and stationary phases without any influence upon the lag phase (sulfonamide compounds, urea and its derivatives, etc.), 3. suppression of all three growth phases (various phenols, acids, alcohols, aldehydes as well as a number of antibiotics), 4. suppression of the stationary phase without modifying the course of the lag and logarithmic phases (streptomycin under a certain experimental condition). According to the mechanism underlying the phenomena, these types of in-

hibition, especially those of 1 and 3, may be further classified into certain subtypes.

For both the prolongation of lag phase and suppression of logarithmic phase, the functional relationship existing between the degree of inhibition (H) and the concentration (G) of antibacterial substances was investigated and it was found that, quite generally, the following relationship holds: $H = G^n / (\Phi^n + G^n)$, where n and Φ are constants characteristic of each substance and test organism under the given condition. On the whole, substances of the same chemical category showed, irrespective of the kind of bacteria tested, the same type of inhibition with approximately equal n -values, while the value Φ often varied considerably according to the bacteria tested and the culture condition applied. It is considered in the discussion that such a systematic survey, though based essentially on overall observations, may provide an effective avenue of approach to the elucidation of action mechanism of various antibacterial substances.

This investigation was made by collaboration of the following workers: T. YANAGITA, T. UYEMURA, Y. SUZUKI, T. SASA and the speaker.

P. W. BRIAN and J. M. WRIGHT
(Welwyn, Herts.)

An Antifungal and Phytotoxic Metabolic Product of the Plant-Pathogenic Fungus Alternaria solani

Alternaria solani is a well known plant-pathogenic fungus, attacking tomatoes and potatoes. We have recently found that several strains produce an antibiotic, which we have named alternaric acid (1). There is evidence that the fungus produces this substance in the tissue of host plants, the phytotoxic properties of the antibiotic being responsible for some of the characteristic disease symptoms.

Alternaric acid is not antibacterial. It is antifungal, the activity being of a rather specific nature. Germination of the spores of some fungi

is inhibited at low concentrations, e.g. *Absidia glauca* and *Myrothecium verrucaria* are inhibited in the range 0.1–1.0 µg/ml. Germination of the spores of other fungi is not inhibited, even by high concentrations, neither is extension of germ-tubes affected for the first few hours, but the antibiotic has a delayed effect, preventing or slowing-down subsequent hyphal extension, resulting in the production of "stunted" growth. This is well seen in *Botrytis allii*; germination is scarcely affected at 200 µg/ml, but stunted forms are produced at 0.1 µg/ml or below.

American workers (2, 3) have produced evidence that *A. solani* produces a toxin in the host plant, which travels upwards, causing lesions on the foliage from which it is impossible to isolate the pathogen. We have found that alternaric acid, introduced in low concentration into the base of cut shoots or into intact plants growing in culture solution through roots, causes black stem and leaf lesions very characteristic of *A. solani* attack. In an analysis of the nature of this phytotoxic effect, we have found that the water-balance of the plant is primarily affected. Three phases can be distinguished in the effect of alternaric acid on water uptake: (i) a short phase of decreased uptake, (ii) a larger phase of greatly increased water uptake, followed by (iii) a gradual decline in the rate of uptake. This is very similar to the effect of lycomarasin (4), the 'wilting-factor' produced by *Fusarium lycopersici*. Alternaric acid is not specific to Solanaceous plants in its toxic effect, so the host range of *A. solani* must be explained by other factors.

Literature

1. P. W. BRIAN, P. J. CURTIS, H. G. HEMMING, C. H. UNWIN & J. M. WRIGHT (1949). *Nature*, Lond., 164, 534.
2. H. R. THOMAS (1948). *J. Agric. Res.*, 76, 289.
3. O. C. WHIPPLE (1938). *Wisconsin Univ. Sum. Doct. Diss.*, 3, 65.
4. E. GÄUMANN & O. JAAG (1947). *Ber. Schweiz. bot. Ges.*, 67, 3.

The paper was read by P. W. BRIAN.

Discussion

E. GÄUMANN: BRIAN has proved that alternaric acid shows a very high *tissue specificity*; patulin is causing the first symptoms in the *vessels*, alternaric acid is causing the first symptoms in the *intercostal fields*, although it has passed through the vessels. Therefore we must think that the tissue specificity in the plant body is nearly as high as in the human body.

E. G. JEFFERYS (Welwyn, Herts.)

Antibiotics in Soil Ecology

Some knowledge of the stability of antibiotics produced by soil microorganisms is a necessary prerequisite for information relating to the natural significance of such substances in the soil. Antibiotics produced by moulds isolated from the soils of Wareham Heath, Dorset, England, have been tested to assess their stability in this acid sandy soil and also for comparison in a neutral light loam.

All the antibiotics used were made up at two low concentrations in 1/10th McIlvaine buffer solution without the aid of organic solvents. These solutions were assayed at intervals during storage in buffer solution:

- a) alone, over the range pH 3.3–6.9
 - b) plus sterile acid washed sand over the same range
 - c) plus sterile or fresh soils at their natural pH.
- The antibiotics used were gliotoxin, griseofulvin, albidin, patulin (expansine) and viridin.

Griseofulvin is stable at concentrations of 3 and 30 p. p. m. over the whole pH range used, while the other antibiotics are less stable at the higher pH levels than at the lower ones. Of these, patulin is the most stable, 200 and 2000 p. p. m., losing no activity after 81 days at pH 3.3 and losing about 60–70 % of their initial activity at pH 6.9 in the same time. Gliotoxin at 20 and 200 p. p. m. loses little activity in 57 days between pH 3.3 and 5.9, while above this pH loss is increasingly rapid,

being complete at pH 6.9 in 20 and 50 days for the low and high concentration solutions respectively. Albidin at concentrations of 3 and 30 p. p. m. is stable at pH 3.3 for 24 days in the high concentration, while activity is lost in about 6 days at the low concentration. At pH 6.9 both concentrations lose their activity in about 6 days. Viridin at 10 and 100 p. p. m. stored in buffer at pH 3.3 loses activity in 37 and 70 days respectively, while at pH 6.9 all activity is lost in about 1 day in both solutions.

Four samples of Wareham soil were used from the profile of one pit. The samples being 1. the peaty layer, 2. the leached layer, 3. the podsol pan and 4. the subsoil. The neutral light loam was from the laboratory garden. The sterile sand used had previously been washed in HCl and rinsed frequently in water. The soils were used fresh and after autoclaving. Only sterilized sand was used.

More rapid inactivation in fresh soil than in sterile soil is at present taken as indicating "biological decomposition," but it is realised that other explanations are conceivable.

The results indicate that while pH is a most important factor in determining the stability of each antibiotic in the soils used, the nature and treatment of these soils is also a decisive factor.

Rapid inactivation of viridin takes place in garden soil and is mainly due to the relatively high pH (7.0). "Biological decomposition" is seen in Wareham 1 and Wareham 3 but not in the other two Wareham soils where the rate of inactivation is similar to that found in sand alone—the rate in sand being more rapid than the rate in buffer solution only. Albidin behaves similarly to viridin in most respects.

Gliotoxin is inactivated at the same rate as in buffer alone, pH having the only effect.

Griseofulvin and patulin, the most stable antibiotics so far tested, show great stability in the four Wareham soils, some "biological decomposition" being noted in Wareham 1 and Wareham 3. Sand has no effect on the rate when compared with the rate in buffer alone. In the garden soil very marked and rapid

"biological decomposition" of both antibiotics took place.

The extension of this work will indicate those antibiotics most stable in soil. Gliotoxin, Griseofulvin and patulin appear at the moment to be the most stable. All antibiotics so far used are more stable in the soil from which the moulds which produce them were isolated, than in the neutral garden soil used for comparison.

J. G. BROWN (Tucson, Ariz.)

Antibiotics in Relation to Some Bacterial Diseases of Plants

Experiments with the antibiotics, penicillin and streptomycin, for determination of their possible effects on certain bacterial plant diseases, have been carried on in the Department of Plant Pathology of the University of Arizona since 1943. Penicillin and streptomycin, both crude and commercial, kill the tissues of crown galls caused by *Agrobacterium tumefaciens*, without injury to adjacent healthy tissues. Streptomycin causes the lethal effect faster than penicillin. It kills oleander galls, resulting from infection with *Pseudomonas tonelliana*. Streptomycin has been successfully used to rid budwood of the blackspot and shot-hole bacterium *Xanthomonas pruni*. The antibiotics have checked necrotic lesions in the giant cactus, due to infection with the bacterium, *Erwinia carnegieana*. Streptomycin does not injure cut potato seed-pieces treated with it for the control of ring rot caused by *Corynebacterium sepedonicum*.

Application of these findings, particularly in connection with crown gall, should prove advantageous in nurseries.

D. GOTTLIEB and P. SIMINOFF (Urbana, Ill.)
The Activity of Antibiotics in Soil

Despite the fact that many microorganisms which are isolated from soil can produce antibiotics when cultured on laboratory media, the synthesis of these compounds in natural soils

has not been proved. Furthermore, even if such antibiotics were secreted into the soil solution they might not effect the biological equilibrium of their natural habitat because of the modifying influence of the soil. The inhibitory activity of antibiotics will vary with their chemical properties. Thus, the basic antibiotics, streptomycin and streptothricin when added to soil, do not inhibit the growth of *Bacillus subtilis* but the acidic materials, clavacin and actidione and the neutral compound, chloromycetin do inhibit the growth of microorganisms. The basic antibiotics cannot be recovered from soil while antibiotic activity can be extracted from soils containing the acidic and neutral compounds.

Some of the inactivation of basic materials can be explained by their adsorption on the soil colloids; they flocculate illite and bentonite clays and X-ray diffraction studies of the precipitated material show a marked expansion of the crystal lattices. Only after the clays have been saturated is any free antibiotic present in the colloidal suspension. The saturation point of the clay or soil depends on the particular soil and clay type and also on the antibiotic. Acidic or neutral clays do not flocculate the colloids nor expand their lattice structure. The basic antibiotics are strongly bound on soil or clay and are difficult to replace with other high molecular weight basic materials. Inactivation is least in light sandy soils and increases in brown loam and black clay loam soils. The organic matter can be important, for muck soils also render streptomycin inactive.

Though the incorporation of an antibiotic producing actinomycete in soil prevents the growth of a susceptible bacteria, such results do not prove the production of antibiotics in the soil. *Streptomyces griseus* in soil prevents the multiplication of *Bacillus subtilis*, yet the result is not due to the secretion of streptomycin, for this antibiotic is inactivated under these conditions and a similar antagonism occurs with mutants of *S. griseus* which do not produce streptomycin.

Since many of the antibiotics which have been isolated are basic compounds, it is ap-

parent that as a group this type might not be biologically active in soil. Such results could explain the failure of many antibiotic producing organisms to control the growth of soil borne plant pathogens in their natural substrate. However, the acidic or neutral antibiotics which were tested remain active in soil and if they are produced there in sufficient amounts could inhibit susceptible organisms.

JOHANNA C. SOBELS (Utrecht)

Culture and Antibiotic Properties of Myxomycetes

It is possible to discern two large groups of myxomycetes.

The first group comprises the myxomycetes which are both parasites and saprophytes. The plasmodia retain under all conditions their orange-yellow pigmentation. They can be easily purified and grown in pure culture by feeding them with sterilised suspensions of micro-organisms (yeasts or bacteria). *Licea flexuosa*, *Badhamia utricularis* (strains: I and II). Pure cultures of *Licea flexuosa* can be grown on an agar medium supplied with soluble food.

The second group contains the parasitic myxomycetes. The plasmodia may lose their yellow pigmentation under definite conditions. They are difficult to purify: after a shorter or longer interval the pure cultures will decline. We have not been able to keep any of these alive as pure cultures. In mixed cultures on a medium favourable for the development of the associated organism, these plasmodia will regain their yellow pigmentation. *Badhamia utricularis* (yellow strain), *Physarum confertum*, *Fuligo septica*.

The plasmodia of mycomycetes on their natural medium prove to have an inhibiting action on the growth of micro-organisms. This fact was suggested by the following observations:

a. In wild cultures of plasmodia the associated micro-organisms do not develop normally.

b. In mixed cultures we have hardly ever observed micro-organisms grouped in colonies.

c. In well-grown cultures of plasmodia we have but seldom noticed the appearance of stray infections.

With the auxanogram method we have shown that the mucous excretions of the plasmodium on the medium as well as the aqueous extracts of these plasmodia possess an inhibiting action on the growth of certain micro-organisms.

According to WAKSMAN this action may be considered as an antibiosis.

We assume that the antibiotic action of the above-mentioned substance is of enzymatic character. It allows of a new view on the problems of life condition and nutrition of myxo-

mycetes. Beside nutrition by simple phagocytosis or diffusion, myxomycetes seem to possess the faculty of attacking certain micro-organisms in order to digest these subsequently. The substance acts as well on Gram-positive as on Gram-negative bacteria, on yeasts and on filamentous fungi. By means of the polyvalent character of this antibiosis the plasmodia possess moreover the power of auto-defence. They are able to adapt and to maintain on very different media. *Badhamia utricularis* (strains: yellow, I and II), *Fuligo septica*, and *Physarum confertum*.

SESSION 10

July 20th, 9 a. m. — noon

Chairman: J. RAMSBOTTOM, Recorder: N. FRIES

SUBJECT:

Various Papers

AGATHE L. VAN BEVERWIJK and
JOHA. WESTERDIJK (Baarn)
*A Survey of the Development and the
Desires of the Collection of the
Centraalbureau voor Schimmelcultures*

The Central Bureau of Fungus Cultures was founded in 1905, and since 1907 the collection has been under the directorship of Prof. Dr. JOHANNA WESTERDIJK.

The collection is constantly growing, it now contains 7,600 strains and species. In 1949, 2,600 cultures were distributed to 33 different countries and 430 identifications were carried out.

We are very grateful to all mycologists who have enriched the collection by sending cultures (*Hymenomycetes*, *Penicillia*, *Myxomycetes*, *Mycosphaerella* species, *Helicosporous Fungi Imperfecti* and many other fungus species were received).

The C. B. S. has to cover part of its costs by selling cultures, therefore we have to consider

not only the scientific value but also the practical use of the cultures in the collection. So we want to be more or less orientated in what general interest there is for special systematical groups.

Of course we are very thankful for the many species of *Hymenomycetes* we have received in recent years, but as our funds are limited and therefore our staff cannot be increased as much as we should like, we have to consider the question whether we shall be able to maintain all these species in our collection. The answer to this question depends largely on the interest there is for these fungi. We shall be grateful to know your opinion in this matter.

Concerning the *Actinomycetes*, we know very well that, because they are classified with the bacteria, they do not belong in a fungus culture collection. Nevertheless, we maintain them at our institute because nowhere else in the world is a collection of *Actinomycetes*, containing also the older species, open to anybody who may need them for scientific or industrial purposes.

The taxonomy of *Actinomycetes* is still far from settled. There are wide differences of opinion between American workers and the Italian specialists in this group, e.g. BALDACC. It is therefore important that the older species that have been described in the course of the last 40 years, should also be maintained for further investigation.

We can never guarantee the biochemical properties of our fungi. The workers of the C. B. S. are all botanists. To extend the Institute with a biochemical department is impossible at the present time, owing to lack of funds. Moreover we think it very important to have a sound basis for the study of morphological and taxonomical problems, especially nowadays when industrialists, biochemists, and other non-mycologists ask our advice and send in their isolates for identification.

Of late years the interest in fungi has increased considerably. Fungi have entered the field of biochemistry (antibiotics, vitamin tests), industry (fungicides) and genetics. The C. B. S. desires to meet as fully as possible the different requests made to this institute, and so we are glad to receive cultures of fungi that have proved to be of interest in these respects.

We wish to express our thanks to those, all over the world, who are contributing to the maintenance and growth of the Centraalbureau voor Schimmelcultures and we sincerely hope that our institute will be able to help in the advancement of mycology.

LEONTINA CAMICI and G. SERMONTI (Roma)

*Morphological Observations on the
Organisation of the Mycelium of Penicillium
Chrysogenum in Submerged Culture*

Morphological observations were made on the organisation of the mycelium of *Penicillium chrysogenum* Q 176 when grown in shake flasks in submerged culture.

In submerged shake cultures the mycelium can organise its growth in two types which differ from each other in their morphological appearance. These will be referred to as "pel-

let" and "filamentous" types of growth, respectively.¹

The "pellet" type of growth is characterized by the mycelium growing in form of small pellets, usually of spherical shape, though occasionally ellipsoidal and irregular forms are encountered. The diameter of the spherical pellets may vary in different cultures from a fraction of a millimeter to several millimeters, depending on the composition of the culture medium and the size of the inoculum, but does not show great variations in same culture.

The "filamentous" type of growth appears in form of a more or less dense, uniform, mucilaginous mass.

The reasons for which the mould mycelium organises itself in these two types of growth have been elucidated by microscopic observation.

In both cases growth of the mycelium starts from a certain number of "growth centres" represented by conidia or hyphae, single or in groups, which are capable of development.

When the number of these centres in the culture medium is relatively small they find themselves at such distance apart that they can develop in relative independence to each other. The growth of the single centres occurs in centrifugal manner in all directions so that each of them develops into a well defined, sub-spherical colony consisting of compact pseudo-parenchymatous mycelium. This is the "pellet" type of growth.

At a later stage of development the spherical pellets become hollow.

When the number of growth centres in the culture medium is large they are crowded close together. The hyphae developing from the centres—the growth of which is limited by competition for the culture medium—come in close contact with each other intertwining in all directions so that a continuous network of mycelium is formed in which it is impossible to distinguish single colonies.

¹ The well known corn steep-lactose culture medium was used for most experiments, but the mould shows similar growth behaviour on other culture media.

This is the "filamentous" type of growth.

Between the two extremes of "pellet" growth and "filamentous" growth intermediate forms occur, consisting of a large number of very small corpuscles the number and size of which depends on the number of growth centres, the size decreasing as the number increases.

In order to obtain reproducible growth behaviour it is essential to take into account not only the size of the initial inoculum, but also the losses of conidia and hyphae on the walls of the culture vessels during the first stages of growth. The shape of the culture vessels is of great importance in this respect.

In both types of growth, after a short time the mycelium begins to degenerate, starting with the older elements, and a continuously increasing number of dead hyphae, devoid of their protoplasmic content, is observed.

In the stromatic pellets this process of degeneration progresses from the centre to the periphery where the youngest cellular elements are located. In time, as the process of degeneration and autolysis proceeds, cavities develop in the centre of the pellet colonies which eventually become completely hollow. At the final stage each pellet colony consists of a spherical layer containing living mycelium in good condition at the periphery and degenerating mycelium towards the central cavity.

In the case of the "filamentous" type of mycelium, dead and living hyphae are randomly distributed in the culture medium. It is obviously of great importance for the qualitative evaluation of metabolic experiments with *Penicillium chrysogenum* and other moulds showing similar behaviour to take into account the amount of dead mycelium present which may be considerable even at the early stages of development.

Discussion

D. GOTTLIEB: The observations of Dr. CAMICI are very similar to those we have made on cultures of *Streptomyces griseus*. In the case of the actinomycete, the mycelium forms a dense

center, parenchymatous in nature. This is surrounded by a periphery of vital intertwining hyphae. The metabolic activities of this organism, as measured by the O_2 is apparently related not to the total amount of fungus material but only to the amount of living mycelium. Thus, as shown in Dr. CAMICI's studies, soon after the growth of the fungi begins there are considerable quantities of dead mycelium even while most of the hyphae are still actively growing.

O. ROBERTS (Cork)

Translocation in the Fungi

The uptake and translocation of sugar and minerals was studied in a number of common moulds by observing their growth from a full nutrient agar on to a contiguous agar deficient in one or more nutrients. *Phycomycetes*, which have no cross walls and show vigorous protoplasmic streaming, grew satisfactorily on the deficient medium and therefore are capable of transporting the substances mentioned.

Penicillium, *Aspergillus* and Basidiomycete mycelia, in which it is difficult to observe streaming, would not grow at all onto a deficient medium. In demonstrating translocation in the *Phycomycetes* temperature and oxygen were shown to be important factors; but the addition of substances which other workers have shown to accelerate streaming did not result in an increased rate, nor did it have any effect on the non-translocating species. Translocation was not markedly affected by the osmotic relationships of the nutrient and deficient agars.

In the Agarics, rapid upward translocation of fluorescein solution at rates up to 2"/hour in definite zones of the stipes was observed. This movement was polar and not observed in old fructifications. The dye was carried up in the pileus in a narrow zone just above the insertion of the gills. In young fructifications this translocation took place in saturated air when no "transpiration" was possible and it was stopped by ether. It is suggested that movement of

materials in the Agaric stipe is by a mechanism comparable to that generally accepted for transport in the phloem of higher plants.

Discussion

W. P. K. FINDLAY asked if experiments on translocation of materials had been studied in strand-forming basidiomycetes such as *Merulius lacrymans* and *Armillaria mellea*, as it is well known that these fungi can transport food materials over long distances (e.g. many metres).

O. ROBERTS replied that experiments had been carried out on these fungi. Translocation of dyes was at the rate of about 2.5 cms per hour in the mycelium. *Armillaria* was a difficult subject as the rhizomorphs are self-fluorescent in UV light.

This work was carried out in collaboration with Dr. KARL SCHÜTTE, Cape Town, South Africa.

ERNA BACH (Köbenhavn)

On Hydrocyanic Acid Formation in Pholiota aurea

Experiments with *Pholiota aurea* (MATT.) FRIES showed that hydrocyanic acid (HCN) was produced when cut pieces of the fruit bodies were stored 24 to 48 hours in air.

Fresh fruit bodies did not contain HCN and production of HCN in the growing mushroom took place only when these had been in some way damaged.

On the other hand grinding or treatment with toluene or alcohol inhibited the reaction.

The production of HCN requires the presence of oxygen.

In a nitrogen atmosphere no production of HCN could be found, whereas the amount of HCN was doubled when a steady stream of oxygen was maintained through the flask as compared to the amount in a closed flask filled with air.

The production of HCN seemed to have a

temperature optimum within a range of 15° to 25° C.

At 0° C small amounts only of HCN are formed and after an increase of the production at intermediate temperatures there is a very marked decrease at 35° C.

A few experiments on heating the cut fruit bodies for shorter periods showed that no production of HCN took place, either during the heating process or during subsequent storage, when the fruit bodies were heated to temperatures above 50° C from 30 to 60 minutes.

The experiments indicate that the formation of HCN in *Ph. aurea* is an enzymatic reaction and that this reaction, if not itself directly the product of an oxidative decomposition, is coupled to oxidative reactions.

The mycelium of *Ph. aurea* is able to form HCN too either when growing on solid substrates or in liquid cultures.

BIRGITTA NORKRANS (Uppsala)

On Cellulolytic Enzymes of Different Tricholoma Species

The photometrical method was applied to determination of cellulolytic activity of extracellular enzymes (or enzyme) from different *Tricholoma* species in cell-free solution on a suspension of finely disperse precipitated wood-cellulose. Sugar-formation, loss in cellulosic matter and changes in average degree of polymerization (D. P.) were determined in addition to the extinction measurements. The enzymes split off water-soluble reducing sugars as well as longer chains of glucose-anhydride-units. Cellobiase seems to be lacking among the extracellular enzymes. The pH optimum for the enzyme activity, as well as the stability against different pH's and temperatures were established. The following types were compared: mycorrhiza-forming and non-mycorrhiza-forming *Tricholoma* species and two wood destroyers [*Polyporus annosus* FR. and *Coniophora puteana* (SCHUM. ex FR.) KARST.] as to the enzyme activity in relation to mycelial total-nitrogen formed.

Discussion

G. FÄHRÆUS:

1. Are the cellulolytic enzymes formed also in the absence of cellulose in the culture medium?

2. Have you tried also pure cotton cellulose as a substrate for the enzyme? In my own experiments with enzymes from bacteria (*Cytophaga*) no attack on cotton could be observed, although cellophane strips were readily hydrolyzed.

3. In the decomposition of cellulose, do you think that the glucose units are split off one by one, or are larger units formed first?

BIRGITTA NORKRANS:

1. The fungi did not form any cellulolytic enzymes when cultivated on glucose, and only small amounts when cultivated on lichenin.

2. A break-down of cotton cellulose to about 6 per cent by these cellulolytic enzymes has been shown.

3. The initial rapid drop of D. P. indicates chainbreaking in central parts of the cellulose chains.

G. LINDBERG (Uppsala)

Different Types of Phenol Oxidases in the Cultivated Mushroom

The mycelium of the hymenomycete, *Marasmius graminum*, forms a copper-containing phenol oxidase of the laccase type. This enzyme catalyzes the oxidation of polyphenols and diamines, e.g. catechol, hydroquinone, and p-phenylenediamine. It is not poisoned by carbon monoxide. The fruit bodies of the cultivated mushroom, *Psalliotia bispora* f. *albida* (= "*Psalliotia campestris*"), contain a polyphenol oxidase, tyrosinase, which oxidizes catechol but not p-phenylenediamine and which is inhibited by carbon monoxide (KEILIN & MANN 1938). Provided that the mycelium of *Psalliotia bispora* contains the same carbon monoxide-sensitive oxidase, it should be possible to clarify the problem if the phenol oxidases of these fungi act as terminal respiratory enzymes. This

might be done by studying the influence of carbon monoxide on the respiration of the mycelia. The respiration of the *Psalliotia* mycelium ought to be sensitive to carbon monoxide whereas that of *Marasmius* ought to be insensitive. Therefore, the mycelia of both fungi were grown in Barcroft vessels and the influence of carbon monoxide on the respiration was determined. Neither of the two fungi was inhibited. Further studies proved that the *Psalliotia* mycelium contains a phenol oxidase of the laccase type as does the mycelium of *Marasmius*. When cultivated in composts, the mushroom forms rhizomorphs, i.e. strings of hyphae, the function of which is to transport substances from the absorbing mycelium to the fruit bodies. Rhizomorphs of *Psalliotia bispora* were proved to contain phenol oxidases of two different kinds, viz. a laccase and a carbon monoxide-sensitive polyphenol oxidase of the tyrosinase type. The fruit bodies, finally, contain only tyrosinase. The significance of the difference between the phenol oxidase formation in the mycelium, the rhizomorphs, and the fruit bodies of *Psalliotia bispora* was discussed.

Discussion

P. DE KOCK: Extracellular and intracellular polyphenol oxidase enzymes may vary widely in character. It seems likely that to be able finally to classify polyphenol enzymes, workers in this field will have to agree on a number of phenolic compounds, e.g. ortho-, meta-, and para-cresols, catechol, tyrosine, and phloroglucinol, which the enzyme will either oxidize in a greater or lesser degree. The influence of inhibitors seems to be of lesser consequence in characterisation, as the same preparation may exhibit different degrees of (cyanide) inhibition as it ages.

W. SCHWARTZ (Mahlum bei Bockenem) *Sedimentbakteriologie*

Bisher ist wenig über die Vorgänge bekannt geworden, die sich bei der allmählichen Umwandlung von Ablagerungen des Süsswassers

und Salzwassers zu Sedimenten abspielen. Mit Rücksicht auf die mikrobielle Entstehung bituminöser Substanzen sind vor allem die Fälle interessant, in denen es sich um Ablagerungen mit einem hohen Gehalt an organischen Bestandteilen handelt. Von Einzelheiten abgesehen, hat sich die Forschungsarbeit auf diesem Gebiet in zwei Richtungen erstreckt: Russische Forscher haben sich vor allem mit der Entstehung des schwefelwasserstoffreichen schwarzen Schlammes und mit seiner mikrozonalen Gliederung beschäftigt. ZOBELL, WAKSMAN und andere haben den Keimgehalt rezenter mariner Sedimente untersucht.

Wir haben festgestellt, dass es möglich ist, mit Hilfe von Modellversuchen Einblick in den ersten Abschnitt der Prozesse, in den Abbau der in den Ablagerungen enthaltenen organogenen Bestandteile, zu erlangen und den Einfluss von äusseren Bedingungen auf die Abbauvorgänge und die Metabiose der verschiedenen Gruppen von Mikroorganismen zu verfolgen. So beeinflussen z. B., abgesehen von p_H und r_H , die Höhe der Wasserschicht, Licht und Dunkelheit, Süss- und Salzwasser stärkstens den Verlauf der Abbauvorgänge und die Anreicherung schwer aufschliessbarer Verbindungen bei gleichem Ausgangsmaterial. Im Verlauf der Umsetzungen treten neben zahlreichen bekannten Mikroorganismen der verschiedenen systematischen Gruppen einschliesslich der Protozoen auch unbekannte Formen auf, wie über-

haupt die Mikrobiologie der Schlammablagierungen und des Wassers reich an Überraschungen ist. Dies gilt vor allem für Bakterien und bakterienartige Organismen. Chlamydobakterien scheinen z. B. wesentlich weiter verbreitet zu sein als man im allgemeinen annimmt, wenn auch oft nur in einzelnen Individuen. Im Oberflächenhäutchen des Wassers trifft man auf Caulobakterien und auf bisher unbekannte Bakterienformen, die sich zum Teil anreichern und in Reinkultur gewinnen lassen. Im Schlamm herrschen zeitweise Clostridien vor, die auf eingestellten Objektträgern reichlich Sternbildungen zeigen. — Die Untersuchung fertiger Sedimentgesteine ist ein zweiter Ansatzpunkt. Selbst in grossen Tiefen sind noch lebende Bakterien gefunden worden (ZOBELL, ISSATSCHENKO usw.). In Erdöllagerstätten haben wir eine autochthone anaerobe Bakterienflora nachgewiesen. In Kohleflözen scheint das Vorkommen autochthoner Bakterien noch immer umstritten zu sein. Eine Untersuchung von interglazialen und postglazialen Sedimenten vom Typ der Braunkohlentone und der Laacher Schicht in einem Braunkohlentagebau am Hils ergab neben wenigen autochthonen Keimen eine starke sekundäre Besiedlung durch allochthone Bakterien und Pilze, wobei erhebliche Unterschiede in der Zusammensetzung der Mikroflora der einzelnen Schichten beobachtet wurden.

Vorgetragen von N. FRIES.

NOMENCLATURE, NOM

Presidents: E. D. MERRILL, T. A. SPRAGUE

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C. G. G. J. VAN STEENIS, ELSIE MAUD WAKEFIELD

Rapporteur Général: J. LANJOUW

Vice-Rapporteur: F. P. JONKER

Secretaries: Mrs. M. L. SPRAGUE (English), W. ROBYNS (French), J. MATTFELD (German)

Recorder: N. HYLANDER

Vice-Recorder: S. AHLNER

REPORT

by J. LANJOUW, Rapporteur Général

The procedure set down for the discussions on the International Rules of Botanical Nomenclature at the Seventh International Botanical Congress, Stockholm 1950, was for the greater part the same as that followed in 1930 at Cambridge and in 1935 at Amsterdam.

The proposed amendments were collected in a volume issued on behalf of the International Commission of Taxonomy of the IUBS under the title "Synopsis of Proposals concerning the International Rules of Botanical Nomenclature submitted to the Seventh International Botanical Congress—Stockholm 1950." Owing to circumstances already explained in the introduction, the publication was retarded, and my hope that it would be available at a more suitable time than the Synopses of Proposals that had been issued in the past, was not fulfilled. The book counted 255 pages and contained 540 proposals. As it proved impossible to set apart more than 40 hours for the discussion, this meant that if all proposals were treated in the same way we would have only about 4 minutes for each of them. However it was clear that quite a number of proposals would require a

very careful consideration, and that therefore a general time limit of 4 minutes would be absurd. For this reason I planned a method for the elimination of a considerable number of proposals, viz. all those of which it was to be expected that they would obtain but little support. With the Synopsis, which was distributed to everyone who was entitled to vote (for particulars on the allotment of votes see below), was enclosed a preliminary voting form on which all proposals were entered. The voter was asked to express for each proposal his approval or disapproval by filling in "Yes" or "No." The delay in the distribution of the Synopsis certainly was a drawback, as it left the voters but little time for a study of the proposals, but I hope that next time this will be different. Another, and perhaps a more serious, objection has been raised against the way in which the proposals were presented. As had been done by former Rapporteurs (although less consistently) I had given in the Synopsis my own opinion on the proposals. It was argued that I may have exercised in this way an undue influence on the results of the preliminary voting, and as this

vote was used for the elimination of proposals, also on the final decisions of the Congress. I will not deny this, but on the other hand it must be understood that it facilitated the choice of the voter who now had to decide between two alternatives, the opinion of the Proposer and that of the Rapporteur. The actual result was that in most (although certainly not in all!) cases the preliminary vote corroborated the opinion of the Rapporteur. For me this result does not prove that I have been able to force my opinion on quite a number of fully competent judges, but only that I am apparently not wholly unfit for the position of Rapporteur. I have dealt rather extensively with these objections, as it is important for a mutual understanding that questions of this kind are openly discussed. With regard to the general principle of the procedure I may add that the majority of the participants of the meetings have signified their approval and expressed their wish that the same line of conduct be followed at future Congresses.

About 200 voting forms were returned to me. As you will see from the minutes it was decided that proposals against which there was a three quarter majority, were to be regarded as rejected. However, if anyone wished to bring in further arguments, the proposal would be brought in discussion. In the same way a proposal with a three quarter majority in favour was automatically accepted; all really important proposals, however, were laid before the meeting. The procedure sketched above enabled us to complete our task in the available time. I wish to state here that the friendly and helpful way in which all participants of the sessions—and especially our Swedish hosts—did their best to lighten my task, was of prime importance for the satisfactory course of the proceedings.

Allotment of votes

As at foregoing congresses the allotment of votes was the task of the Swedish Organizing Committee. Institutes, Societies, etc. were given

one to five votes according to their relative importance in the field of taxonomic botany. The list prepared by the Organizing Committee was sent to me in order that I might suggest alterations or additions, an opportunity of which I have availed myself to a slight extent only. Further one vote was given to each officer of the Section, one vote to each member of a nomenclature committee, and one vote to each individual botanist who had proposed one or more amendments to the Rules. The Institutes etc. as well as individual persons received from the Swedish Committee a form in which they were notified of the number of votes to which they were entitled, and they were invited to return another form, attached to the one first mentioned, on which they were asked to acquaint the Committee with the name of the person who was going to represent them at the Congress. These forms were sent to me by Dr. ÅBERG, the Swedish Secretary, so that I was able to make a card index of all botanists who would be entitled to vote. Several days before the Congress I established an "Office for Nomenclature" at the Congress Headquarters at Stockholm. At this office the members of the section received the necessary information, copies of the Synopsis and of original proposals accompanied by the comments of the proposers, voting books and voting cards. The latter were yellow cards (red for Paleobotany) on which were mentioned the name of the voter and the number of votes to which he was entitled. They were to be used during the sessions for voting by "show of cards."

A mimeographed copy of the complete list of votes was available at the sessions of the Section.

Procedure during the Sessions

The "Bureau of Nomenclature" (see in the minutes for its composition) came together for the first time shortly before the first session, and it met several times between the sessions. Various questions were discussed with regard to the procedure to be followed at the sessions.

On Thursday July 6th, in the evenings of the

other days and on Sunday July 9th there were various meetings of the subcommittees on which proposals concerning their special domain were discussed. As far as I know, this was the first time that the special committees (apart from that for Palaeobotany) met in this way. Special mention should be made of the work done by the committees for "Typification", "Palaeobotany," "Fungi", and "Nomenclature of Cultivated Plants." It meant an extra burden for those who acted on these committees, but it may console them for their lack of sleep that they helped to reach results of prime importance. The reports of their painstaking work belong to the most valuable achievements of the Section.

The minutes of the discussions held during the general sessions were made by Mrs. M. L. SPRAGUE when they took place in English, by Prof. W. ROBYNS when they were in French, and by Prof. J. MATTFELD for those in German. Prof. ROBYNS, moreover, acted as interpreter for French, and Prof. MATTFELD for German, while Dr. WILLIAMS kindly assisted us by translating from and into Spanish. Mr. FLORSCHÜTZ and Mr. MENNEGA acted as scrutineers, and collected the notes the participants in the discussions were asked to write down. As most of the discussions were held in English it will be understood that the task of Mrs. SPRAGUE was a particularly heavy one. The minutes of the dis-

cussions are based on the following documents: a report in English by Mrs. SPRAGUE, a report in French by Prof. ROBYNS, a report in German by Prof. MATTFELD, a report made by Dr. DE WIT for personal use, and various notes by Dr. JONKER, by Mr. FLORSCHÜTZ and by myself, but we may safely say that it rests for 80 to 90 per cent on the work of Mrs. SPRAGUE. A salute of honour to her; without Mrs. SPRAGUE a meeting on Botanical Nomenclature would hardly be thinkable!

It is perhaps not superfluous to add that in order to understand the minutes of the discussions it is highly desirable to consult the following two publications.

J. LANJOUW, *Synopsis of Proposals concerning the International Rules of Botanical Nomenclature submitted to the Seventh International Botanical Congress—Stockholm 1950.*—I. U. B. S. 1950.

J. LANJOUW, *Botanical Nomenclature and Taxonomy. With a Supplement to the International Rules of Botanical Nomenclature, embodying the alterations made at the Sixth International Botanical Congress, Amsterdam, 1935,* by T. A. SPRAGUE.—*Chronica Botanica*, Vol. 12, 1/2—1950.

To the present report are added five supplements. They contain the decisions of various special committees as accepted by the Congress, and a list of the voters.

DISCUSSIONS

Minutes mainly based on the Report made by Mrs. M. L. SPRAGUE

SESSION 1

July 7th, 9.30 a. m. — 12.15 p. m.

Chairman: E. D. MERRILL

Prof. MERRILL opened the proceedings by saying that although both he and the other President, Dr. SPRAGUE, had prepared speeches neither of them proposed to give them. He

asked the members to stand as a token of respect to the memory of the many botanists who had died since the last Congress.

Prof. MERRILL then read the following ex-

tract from a letter which he had received from the late Dr. WEATHERBY after the Utrecht Conference:—

"I thank you for the copy of the Report on the Utrecht Conference. It brings, however, a certain feeling of depression. Nomenclature is taking much time and effort, and is becoming too technical. The Rules are in danger of becoming so clogged with matters of detail which ought to be looked after by a nomenclatural commission, that if we do not look out we may well develop a group of botanist-lawyers to interpret them. No one will be able to bear their provisions in mind. I am near enough to being a professor of nomenclatural law myself to dislike the idea very much."

Prof. MERRILL explained that he himself was impressed with these ideas and hoped that they would serve as a guide in the discussions. He then asked the *Rapporteur-général* (Prof. LANJOUW) to announce the procedure to be followed in the discussions.

Prof. LANJOUW referred to the preliminary voting on the proposals in the Synopsis, and suggested that those proposals which had a 3/4 majority against them should be automatically rejected, unless cause could be shown for discussion, and that those which had 3/4 majority in favour should be automatically accepted, the Editorial Committee being left to draft the final text.

Prof. MERRILL then moved that these proposals made by Prof. LANJOUW should be accepted in principle.

This was approved.

Mr. ROSS suggested that any proposal rejected in the preliminary voting by a majority of more than 3:1 which the relevant Special Committee wished to be discussed might be brought up.¹

Prof. MERRILL then read out the list of members of the Bureau of Nomenclature:—

Presidents: Prof. E. D. MERRILL; Dr. T. A. SPRAGUE.

Recorder: Dr. N. HYLANDER.

Vice-Recorder: Dr. S. AHLNER.

Rapporteur-général: Prof. J. LANJOUW.

Vice-Rapporteur: Dr. F. P. JONKER.

Secretary for English: Mrs. M. L. SPRAGUE.

Secretary for French: Prof. W. ROBINS.

Secretary for German: Prof. J. MATTFELD.

Prof. MERRILL then asked for the approval of the proposed Bureau.

Approval was unanimous.

Prof. LANJOUW then asked the section to approve the alterations made in the Rules at Amsterdam and later at Utrecht.

Dr. DONK suggested that the Congress should not delegate too much of the phrasing or the re-casting of accepted proposals to the Editorial Committee. In the past that Committee had taken some liberties that are not in agreement with what had been decided during the sessions. The present wording of Art. 37 bis is a telling example of this unhappy situation. The differences will become clear if one compares the wording as presented in the "Brittonia" Edition of the Rules and that printed in the Synopsis. The last example but one under Art. 37 bis (Synopsis) is written in anticipation of a proposal put before the present Congress by Dr. SPRAGUE. The phrasing of the main body itself looks rather like a personal interpretation too. (*Note*—Actually all the examples were appended to the Article when it was first proposed in 1929, in "Proposals by British Botanists" pp. 16-17 as Art. 44, and were duly included in Briquet's "Recueil Synoptique" 1930, pp. 41-42, as Art. 37 ter—Ed.)

Certain questions were then asked about particular cases such as Art. 37 bis and Rec. XLIII which it was stated were not quite in conformity with the text as adopted in Amsterdam.

Prof. LANJOUW explained that he and Dr. SPRAGUE had slightly altered the text to what they considered a better rendering of the Rules and Recommendations, but that when these particular points came up they could be discussed.

Dr. ROUSSEAU proposed that amendments as

¹ Actually the procedure has been that all Special Committees in their reports to the Section were free to include any matter which seemed to them useful for improvement of the Rules. Thereby any proposal rejected in the preliminary vote could be taken into consideration—J.L.

voted at Amsterdam should be adopted with the reserve that they might be open to discussions. Also that in future we should resume the practice of printing the rules in English, French and German.¹

Prof. MERRILL explained that all that was needed at this stage was *general approval* of the Supplement and of Professor LANJOUW's Synopsis. This was put to the vote and was carried unanimously.

Dr. RAMSBOTTOM urged that the Section should not consider mere grammatical alterations in the Rules but solely principles. Points arising could be dealt with by the Editorial Committee. All members having corrections to suggest should hand them to the Secretary.

Dr. ROUSSEAU seconded Dr. RAMSBOTTOM's proposal, and it was carried unanimously.

Dr. FOSBERG then asked if the Rapporteur would give the final preliminary vote in all cases. This was agreed and Prof. LANJOUW explained the system of procedure still further.

The various proposals were then taken in order.

Article 1

PROP. 1 (36:245)² Rejected.

Dr. DONK said that although this proposal had not obtained sufficient preliminary votes, he wanted to cast a vote for its acceptance. The rules are the self-appointed trustees of the nomenclature system introduced by LINNAEUS and the statement of this fact in the Rules does not seem superfluous. If this point of view had been adopted long before as a guiding principle, it would have been easier to recognise the fact that the Rules are a mixture of several different systems of nomenclature. At present they admit (1) the overflow of Tournefortian generic names (such as are not associated with

specific epithets) after 1753; (2) ADANSON's names which are uninomial; (3) and certain conventional—rather pseudo-Linnean—systems of nomenclature for hybrids, lichens, Fungi Imperfecti and certain fossil plant remains.

The correct distinction of these admixtures would be helpful in wording the divisions of the rules that deal with them. It is true that the present rules are not Linnean System, but the wording of the proposal takes care of that by stating that it *shall be known as such*.

Dr. SPRAGUE said it was undesirable to make the Rules long and complicated. There might be a separate Commentary explaining any points which required further elucidation.

Dr. RAMSBOTTOM said that Rules should be as concise as is consistent with clarity. Possibly some form of official commentary on the Rules might be useful. In this, the various examples illustrating the Rules might be placed.

Prof. MERRILL agreed that a commentary might be useful. He considered some of Dr. FURTADO's suggestions very clear and good, but too long to be included in the Rules themselves. He then asked Dr. DONK if he was satisfied.

Dr. DONK: Not for this article.

Dr. BLAKE considered that the present Art. 1 in its reference to "a precise system of nomenclature which is used by the great majority of botanists in all countries" sufficiently identified the Linnaean System.

Dr. ROUSSEAU speaking in French, said that the existing Rules of Nomenclature were those of LINNAEUS only in so far as the binominal system was concerned. The majority of the seventy-four Rules were neither formulated nor followed by LINNAEUS.

Prof. MERRILL suggested that the whole Article be entrusted to the Editorial Committee.

Dr. CAMP asked that a vote should be taken on the Article.

Prof. HOCHREUTNER speaking in French, asked for further information. The system of voting was again explained by Prof. LANJOUW.

Prof. MERRILL then put Art. 1 Prop. 1 (FURTADO) to the vote by show of cards, and it was

¹ The Editorial Committee will prepare first a complete new text in English. It is provided for to make at the same time texts in French, German and probably Italian and Spanish.

² The figures refer to the preliminary vote on the Synopsis of Proposals distributed before the Congress to all who were entitled to vote. The first figure gives the number of votes in favour of the proposal, the second one gives those against.

rejected by a very large majority, only 2 being in favour.

Article 2

PROP. 1 (251: 1) *Accepted.*

PROP. 2 (14: 142) *Rejected.*

PROP. 3 (13: 245) *Rejected.*

Article 4

PROP. 1 (134: 84)

Prof. MERRILL suggested that this should be referred to the Editorial Committee.

Prof. LAM proposed that the reference should be with power to amend the wording. This was seconded and passed by a very large majority. At Dr. CAMP's suggestion, both the first and the final preliminary voting were read out for a large number of Articles by Prof. LANJOUW, but as this took so much time, Dr. BLAKE suggested that if the revised figures were given only where the vote was close or where there was any significant change, much time would be saved.

Prof. LANJOUW said he would give the final voting only as each proposal came up.

PROP. 2 (124: 94)

Prof. LANJOUW drew attention to his rewording of this proposal of MANSFELD and ROTH-MALER, namely "Other considerations, such as absolute grammatical correctness, adequacy, regularity, or euphony of names, regard for persons etc. are of no weight in questions of nomenclature."

Prof. MERRILL proposed that there should be a vote on the acceptance of the Proposal, referring it to the Editorial Committee.

Dr. SPRAGUE suggested the amendment "are relatively unimportant."

Prof. MARTIN considered the words "of no weight" not the same as "relatively unimportant."

Prof. MERRILL then suggested that Art. 4, Prop. 2, be sent to the Editorial Committee.

A vote by show of cards was taken and this was carried by a very large majority.

Dr. FOSBERG then pointed out that the matters being referred to the Editorial Committee were not always mere textual amendments.

Prof. PAPENFUSS urged that the rewording of Art. 4, Prop. 2 be not left to the Editorial Committee.

Prof. ROLLINS considered that, wherever possible, decisions should be made by the Congress instead of being referred to the Editorial Committee.

Prof. LANJOUW again read the proposal as he had amended it.

Prof. HOCHREUTNER speaking in French, said he believed it was better to keep the original text wherever possible, as it was familiar to taxonomists. Change should be avoided, even if it resulted in a slight improvement.

Prof. LANJOUW agreed, but thought if minor changes were necessary for clarity, it was better to make them.

Prof. LAM thought the question of whether to use "of no weight" or "relatively unimportant" was a textual amendment.

Dr. RAMSBOTTOM said that the point at issue is not the text of the Article which should be left to the Editorial Committee, but the proposed alteration of the Article, the alternative rendering "of no weight" or "relatively unimportant."

Prof. LANJOUW asked for a vote on his proposal.

Dr. SPRAGUE said that there were three points to be considered:

- 1) Should the original text be retained;
- 2) or be modified as proposed by Prof. LANJOUW;
- 3) or be modified as proposed by himself.

Prof. MERRILL ruled that there should be a vote on 1), whether Art. 4 should be modified or not.

A vote was then taken and a *large majority was in favour of keeping the Article as it stands.*

Article 5

PROP. 1 (18: 209) *Rejected.*

Article 7

PROP. 1 (4: 231) Rejected.
PROP. 2 (22: 222) Rejected.

Article 8

PROP. 1 (225: 19) *Accepted*.

New Article 8 bis

PROP. (224: 25) *Accepted*.

Dr. CAMP spoke on the type concept and referred to a written comment he had sent to Prof. LANJOUW on certain proposals for alterations. He stated that the "circumscription" of a group had nothing to do with the type concept. It was the type of a name and the type alone that mattered.

Dr. SPRAGUE thought that Dr. CAMP had misunderstood the meaning of the word "circumscription" as used in the Rules. It meant what was actually contained in a particular taxon. This was a matter of taxonomic opinion, and until it was decided, the type-method could not be applied. The name of a taxon might have to be changed if a particular element were excluded.

Prof. MERRILL then asked for a vote on the acceptance of Art. 8 bis.

A show of cards gave a *unanimous vote in favour*.

Dr. BOIVIN said that although he was in favour of Art. 8 bis, illegitimacy is not defined in Art. 60 but in Art. 2.

The second sentence of Art. 8 bis should be deleted or modified accordingly. The modification might be left to the editors because of future proposals.

Prof. LANJOUW was in favour of leaving the new Art. 8 bis, including the definitions, after Art. 8.

Dr. Fosberg wished to change Dr. BOIVIN's modification to "Art. 2, expanded in Art. 60."

Dr. RAMSBOTTOM thought Art. 2 and Art. 60 might be combined.

Dr. BOIVIN suggested that Art. 16 should be included as well, and that all these matters might be left to the Editorial Committee.

Dr. ROUSSEAU wished Art. 8 bis to be included in Art. 2, or immediately after Art. 2.

Prof. LANJOUW still thought it was better to leave it as 8 bis after Art. 8.

Prof. MERRILL asked whether this could not be referred to the Editorial Committee.

Dr. BLAKE suggested that Art. 8 bis be laid on the table and taken up later, as many had not had the opportunity to study the proposals sufficiently.

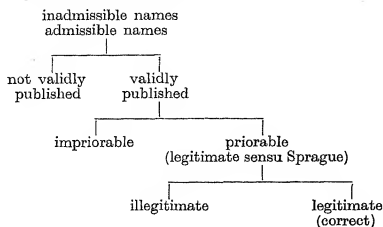
Dr. HYLANDER suggested leaving out Art. 2 and placing the new Art. 8 bis as Art. 2 bis.

Dr. SPRAGUE said that a legitimate name was not necessarily the correct name of a taxon with a particular circumscription, position and rank. Before a name could be considered for acceptance it must satisfy certain conditions: it must be 1) effectively published, 2) associated with a description, i.e. validly published; 3) legitimate, i.e. in strict accordance with the Rules. The correct name of a taxon could not be determined until the contents, i.e. circumscription of the taxon had been decided (a matter of taxonomy). The various legitimate names (if more than one) which had been given to the particular taxon or to any of its elements of the same rank were then considered, and the one which must be adopted under the Rules was the correct name; the correct name being the earliest legitimate name.¹

Dr. DONK drew attention to the fact that the word "legitimate" as used in the Rules corresponds to "priorable" of FURTADO, and that "correct" corresponds to his use of "legitimate." He considered that the wording of Art. 8 bis was highly ambiguous, or rather erroneous. Under the Note the term "legitimate name" becomes identical with "correct name," because to arrive at a correct name one has also to remain "in strict accordance with the Rules." The acceptance of Art. 8 bis as worded in the Synopsis would become a source of confusion.

¹ The word "earliest" has to be inserted in the proposal.

He explained FURTADO's terminology by writing the following table on the blackboard:



Prof. MERRILL suggested that the definition of the term "illegitimate name" be referred to the Editorial Committee.

Dr. HYLANDER stated that illegitimate names were those which were not in accordance with the Rules.

Dr. ROGERS suggested a vote on Art. 8 bis, leaving the insertion of numbers to the Editorial Committee.

Prof. MERRILL put this motion to the vote and it was accepted almost unanimously by show of cards.

SESSION 2

July 7th, 2—5.15 p. m.

Chairman: E. D. MERRILL

Prof. MERRILL made a statement in connection with the Editorial Committee, emphasising the fact that the Committee was not yet appointed, but would be appointed by this Section before the end of the Congress. He hoped that new rules would be written not only in English, French and German, but perhaps in Spanish as well.

Article 9

PROP. 1 (216: 24) Accepted.

Article 10

PROP. 1 (173: 65) Accepted.

Prof. PAPENFUSS: In connection with Art. 10, Prop. 1, I propose the substitution of the designation "*phylum*" for "*divisio*" or the substitution of the words "*phylum or divisio*." This will not only bring the hierarchy of botanical categories into line with that used by zoologists but at the same time bring into usage a term which has more meaning than "*divisio*."

Prof. LAM disagreed with Prof. PAPENFUSS.

"*Divisio*" is an indifferent term, "*phylum*" involves a phylogenetic significance. We might add "and *phylum*." "*Phylum*" (-on) may in future be wanted for a unit in Phylogeny.

Dr. SPRAGUE said that WETTSTEIN's "Handbuch der systematischen Botanik" has both "*phylum*" and "*divisio*." The two terms are not synonymous in his classification.

Dr. HYLANDER supported the proposal to substitute "*phylum*" for "*divisio*," and also (in Art. 12) "*subphylum*" for "*subdivisio*." He considered that the term "*taxa*," as used in Art. 10, Prop. 1, should be changed to "*categories*." He thought that the first sentence required rewording, since hybrids and chimaeras also belong to higher categories, in most cases to a genus, and in any case to a family etc.

Dr. ROGERS said that *Pteridophyta* was an example of a division which was not a phylum.

Prof. HOCHREUTNER speaking in French, said that he was opposed against the introduction of a new term for an old concept.

Prof. LANJOUW thought that Prof. HOCHREUTNER had not understood the right meaning of taxon; it was another name for a taxo-

nomic group. He had had some comments in letters on the word *taxon*, one correspondent objecting to the word because it was not in any dictionary. It was, however a very convenient word, and after two years 60 % to 70 % of botanists were using it.

Dr. HYLANDER supported the acceptance of the word *taxon*.

Mr. ROSS thought that the word "consecutive" was inappropriate in Art. 10, Prop. 1, since the ranks enumerated ceased to be consecutive when such ranks as Tribes, Subgenera are interpolated.

Dr. RAMSBOTTOM asked if the motion could be accepted and then go to the Editorial Committee.

Prof. LANJOUW suggested that the reference to a hybrid or chimaera should be left out of the article.

Prof. LAM disagreed with this.

Dr. HYLANDER suggested the wording "Each individual plant belongs to a species or it is an interspecific hybrid or chimaera. Each species belongs to a number of categories of consecutive rank etc."

Prof. BREMEKAMP referring to the commentary given by the Rapporteur on the Proposal said that the advantage of the term "central taxon" instead of "basic taxon" lay in the fact that there is not only an ascending series of taxa, but also a descending one. He considered that the individual plant is a concept that is difficult to define, and it is therefore better to avoid the use of the term.

Dr. DONK agreed with Prof. LANJOUW that the clause "or it may represent a hybrid or a chimaera" should be left out. The question should be treated in a special part of the Rules devoted to the nomenclature of hybrids, chimaeras and the like.

Prof. LAM: Would it do any harm if left here?

Prof. LANJOUW: A way out of the difficulty might be to put a paragraph in the proposed special Supplement dealing with hybrids.

Prof. LAM: And to put also "see Art. so and so."

Dr. RAMSBOTTOM agreed with Prof. LAM.

Dr. BLAKE considered Art. 10 better than Art. 10, Prop. 1, and suggested that Art. 10 be retained in its present form.

Dr. BORVIN moved that Prop. 1, of Art. 10 be adopted as amended by the Rapporteur.

Prof. MARTIN reverting to the suggestion of Prof. PAPENFUSS, said that the terms *division* and *phylum* are alternatives. Either one cannot be exactly replaced by the other, either should be permissible.

Prof. LAM suggested the wording "*divisio* and *phylum*."

Dr. FOSBERG saw no objection to the use of both terms.

Dr. ROGERS said that *Pteridophyta* was a division but not a phylum; *Archegoniatae* is a phylum but not a division. The two are not interchangeable.

Mr. ROSS: If some botanists wish to divide the plant kingdom into a number of divisions, and others to group the divisions into phyla, the point is covered by Art. 12, last sentence.

Dr. RAMSBOTTOM said that the term *phylum* has often phylogenetic significance which *divisio* has not. If the two terms are really synonymous, *phylum* might be adopted because of its wide use in botanical schools. If a higher rank is needed, *phylum* would be useful assuming that it could be denuded of all phylogenetic implications.

Prof. HOCHREUTNER speaking in French, said that we will have to consider the problem of translation. At present both words "*phylum*" and "*division*" are translated in the French text of the rules into "*embranchement*."

Prof. MERRILL asked Prof. HOCHREUTNER to make his point clear to the French member of the Editorial Committee.

Prof. BAEINI, speaking in French, suggested that the word *phylum* has many meanings.

Prof. ROBYNS maintained that the term *divisio* was understood, but that the term *phylum* was not understood, and he wished that a vote should be taken in accordance with Dr. RAMSBOTTOM's suggestion.

Dr. FOSBERG objected to the adoption in the rules of two alternative terms for the same

category. He also stated that phylum was proposed in Art. 10, Prop. 3, and thought that we should vote on these items in their proper order to avoid the confusion of issues.

Dr. ROGERS disagreed.

Dr. HYLANDER pointed out that a term was needed for the highest category, and the question was, should this be *divisio* or *phylum*.

Prof. LANJOUW said that before anything else we must vote on whether the Article stands in its original form or in the amended one. This led to some discussion on how the voting should take place.

Dr. SPRAGUE thought we should vote first as to whether we should keep Art. 10 as it stands and afterwards vote as to the change.

Mr. ROSS thought that we should vote on each proposed amendment and, if we want the Article unchanged, defeat them. To vote on whether or not we want the Article changed is to telescope votes on all amendments. They should be considered separately.

Dr. RAMSBOTTOM maintained that there was a point as to whether the Article should be changed or not.

Dr. BOIVIN thought the procedure might be speeded up if we voted on the last proposal (namely Prop. 1).

Prof. MERRILL put to the vote *Art. 10, Prop. 1 as amended by the Rapporteur*. This was carried by show of cards.

PROP. 2 (143: 28)

Prof. LANJOUW explained that this referred to *Paleobotany*, and that the Section should have the views of that Committee.

Dr. RAMSBOTTOM referring to the comment of the Rapporteur on Prop. 2 that instead of "fossil plants" we should read "botanical fossils," said that he did not agree that this was an improvement. He suggested that the Paleobotany Committee should settle this question.

Prof. MERRILL asked if all agreed.

This was carried by show of cards.

Dr. DONK suggested that the situation in regard to *Fungi Imperfecti* was somewhat

similar to that of fossil plants, and that the proposal should be discussed in that connection. He went on to explain that although *Fungi Imperfecti* are classified as if they were natural species in a graded system, the fact remains that they are not true species and their names have a restricted legitimacy ("priority").

Dr. RAMSBOTTOM suggested that the Mycological Committee should deal with this.

Prof. MERRILL ruled that that be so.

PROP. 3 (45: 170)

Prof. LANJOUW explained that this dealt with the term "*phylum*".

Dr. RAMSBOTTOM suggested that a vote on Art. 10, Prop. 3, should be taken immediately.

Prof. MERRILL supported this.

Prof. LAM wished to know whether "*divisio*" and "*phylum*" are synonymous. He also said that "*phylum*" might be used in future by phytogeneticists.

Prof. LANJOUW: Let us vote on Art. 10, Prop. 3.

Prof. MERRILL: We will take a vote by show of cards.

The voting was against the proposal by a large majority.

Prof. PAPENFUSS wished for another opportunity to substitute the term "*phylum*" for "*divisio*."

Prof. LANJOUW: But the term "*divisio*" has been adopted.

After a speech by Prof. HOCHREUTINER given in French, Prof. LANJOUW suggested that there should be two votes (1) "instead of *divisio* read *phylum*" or (2) "either *divisio* or *phylum*."

Prof. ROBYNS once more emphasised that the term *phylum* had different meanings in French and English.

Prof. MERRILL ruled that a vote be taken as to whether *phylum* should be used in place of *divisio*.

The result by show of cards was against the motion. *Phylum* should not be used in the place of *divisio*.

Prof. LANJOUW then suggested that a ballot

be taken as to whether the words "divisio or phylum" should be substituted for "divisio."

Ballot	Against	216
	For	103

Prof. ROLLINS suggested that to save time we should stick to the 3/4 majority.

PROP. 4 (11: 189) Rejected

PROP. 5 (34: 126)

Dr. RUTH PATRICK pointed out that in *Algae* the term "individual plant" was not very suitable as the characters in *Algae* are built on the colony.

Dr. SPRAGUE: Could we say every plant?

Dr. PATRICK: Yes.

Prof. LANJOUW moved that the wording should be "every plant" as suggested by Dr. SPRAGUE.

Prof. MERRILL called for a vote by show of cards.

This was carried unanimously.

PROP. 6 (18: 190) Rejected.

Dr. CAMP explained that the word *chimaera* was causing a lot of difficulty.

Prof. LANJOUW pointed out that some members of the section wanted our system of voting discussed, some wanted a vote taken as to whether the present article should be changed, others wanted to vote on the proposals. He thought that since the proposals were sent in for consideration by the Section, the Section ought to vote on them.

Prof. MERRILL: Shall we have the final vote first?

Dr. RAMSBOTTOM thought the proposal should be considered.

Dr. ROGERS thought we should vote on all proposals that received less than 3/4 and more than 1/4 preliminary vote.

Dr. ROUSSEAU supported this.

Prof. MERRILL put the proposal of Dr. ROGERS to the vote by show of cards.

This was carried.

PROP. 7 (3: 233) Rejected.

Article 11

PROP. 1 (161: 60)

Dr. BLAKE suggested that Prop. 1 and 2 of Art. 11 are alternative proposals.

Prof. LANJOUW gave the preliminary voting of Prop. 2, namely (17: 209).

Dr. HYLANDER explained his proposal (Prop. 2). The definition of the term *f. spec.* (special form), mentioned in Art. 11 should be given in the same rule (or in an additional note), not in a recommendation as at present.

Modifications should be left out; "races" and "biological forms" are ambiguous terms and should not be mentioned in the Article.

Prof. LAM suggested that the two proposals should be combined, the useful part of Dr. HYLANDER's Prop. 2 to be included in his proposal (Prop. 1). Prof. LAM also said he was prepared to leave out of his proposal the reference to "*forma biologica*."

Dr. RAMSBOTTOM suggested that these *special forms* could be dealt with by the *Mycological Committee*.

Prof. MERRILL asked if it was the wish of the Section that these be sent to the *Mycological Committee*.

A vote by show of cards showed agreement.

Mr. ROSS suggested that the two proposals 1 and 2 be taken separately.

Prof. PAPENFUSS asked whether in the sense of the recommendations expressed in Art. 11, Prop. 1, do we thereby accept "*varietas*" as a category below "*subspecies*." Many modern botanists regard these two terms as synonymous.

Dr. FOSBERG suggested that *all* modern systematists do not regard subspecies and varieties as synonymous, and he moved that the word "race" and "modification" (*modification*) be deleted from Prop. 1.

Dr. CAMP proposed that action be deferred on Prop. 1 and 3 of Art. 11 until the authors (and others in consultation with them) can present a more satisfactory wording.

Dr. RAMSBOTTOM seconded that proposal.

Prof. MERRILL moved that action should be deferred until another text be brought in.

Dr. DONK said that the proposal might be interpreted in such a way that one might think that a *forma* is to be divided into *formae biologicae*, a *forma biologica* into *formae speciales*, and a *forma specialis* into *modificationes*, compare the words "consecutive downwards" "intercalate intermediate taxa" and "series." It can hardly be the intention to consider these categories as members of a graded series.

Prof. LANJOUW suggested that the word "or" could be included in the text where it was necessary to make it clearer.

Dr. RAMSBOTTOM said this was merely editorial.

Article 11

PROP. 3 (2: 215) Rejected.

New article 11 bis

Awaited paleobotanical report.

Recommendation I

PROP. 1 To the Mycological Committee.

Article 12

PROP. 1 (181: 54)

Dr. RAMSBOTTOM considered that this proposal required rewording. He suggested that the words "to sixteen degrees" be deleted as unnecessary.

Dr. SPRAGUE pointed out that the term "*taxa*" (or "*taxon*") used seven times in Art. 12, Prop. 1, should be replaced by "categories" (or "category"). Families, genera, species are categories of taxa, examples of the corresponding taxa being *Ranunculaceae*, *Rosa*, *Trifolium pratense*. Prof. LAM explained that Dr. RAMSBOTTOM's objection is met in the next paragraph: "if this list of taxa is insufficient, it may be augmented by the intercalation of supplementary taxa, provided that this does not introduce confusion or error."

Dr. RAMSBOTTOM replied that he merely wished to delete the number "sixteen."

Dr. SPRAGUE once again explained the difference between category and taxon.

Prof. LANJOUW suggested that the words "provided that this does not introduce confusion or error" might be deleted.

Dr. FOSBERG: Why?

Prof. SINGER thought that the phrase "provided that they do not introduce confusion or error" should be left in because such confusion may arise, e.g. by the use of the word *series* which is used in different senses.

Mr. ROSS: The position of *tribus* and *sectio* should be defined in the body of the Article and not just in the list at the end. This should be considered in a new draft.

Prof. PAPENFUSS moved that the term "*taxa*" should be defined.

Prof. LANJOUW replied that a definition of the term could be found in Art. 8, Prop. 1.

Prof. LAWRENCE suggested that examples should be added.

Prof. MERRILL suggested that *action be deferred* until a new draft of the proposal be forthcoming, and this was agreed.

PROP. 2 (17: 92) Deferred.

PROP. 3 (39: 169) Already dealt with.

PROP. 4 (2: 214) Rejected.

PROP. 5 (88: 114) Already dealt with.

PROP. 6 (26: 177) Already dealt with.

PROP. 7 (164: 45)

Dr. FOSBERG considered that the introduction of a category such as apomict is the introduction of descriptive material into nomenclature as a species, variety, form or any other lower category may be apomictic. If such things are introduced into nomenclature there is no place to stop, all types of species are equally susceptible then to such separate designation.

Prof. MERRILL then asked Dr. CAMP if he would care to speak on his proposal.

Dr. CAMP pointed out that there is a large number of cytotaxonomists and experimental

¹ Because that has already been said in Art. 4. It is needless to state every time that "confusion or error" must not be introduced, for that alone does not prevent them.—J. L.

taxonomists who must have their need for additional categories considered.

Dr. SPRAGUE asked whether the wording "other types of categories may be intercalated" would meet the case.

Dr. CAMP considered that would be a useful addition.

Dr. FOSBERG emphasised that the term apomict was "characteristic."

Dr. BOIVIN thought it was a category.

Dr. HYLANDER suggested that a note might be added to the article regarding other categories such as apomicts, etc.

Prof. ROLLINS emphasised that this was a real problem. He said apomicts are now being designated as species and thus it would be useful to have the category apomicts.

Dr. FOSBERG suggested that Dr. CAMP had proposed 15 kinds of species.

Dr. CAMP said they were just preliminary species.

Prof. ROLLINS considered that we should try and be practical in our nomenclature.

Prof. BREMEKAMP thought that there was no place for apomicts etc.

Prof. ROBYNS considered that we should concern ourselves with floristic groups.

Dr. RAMSBOTTOM considered that something must be done to meet the needs of the horticulturists, etc. We are dealing with the Rules of Nomenclature he said, the point for us to consider is what form of nomenclature should best be applied to apomicts, etc. The thousands of binomials which are being published may be reduced, but not by those workers in these special subjects.

Dr. CAMP expressed his gratitude to Dr. RAMSBOTTOM for his remarks. He went on to say that the name of the apomict might be bi- or trinomial. There is an increasing group of experimentalists who are getting very discontented and he thought that if nothing were done in this connection there would be two sets of Rules.

Dr. HYLANDER thought as Dr. CAMP had agreed to prepare the Rules for hybrids etc. this matter might also be referred to him, and

that a reference to that chapter might be inserted here.

Dr. RAMSBOTTOM agreed with Dr. HYLANDER.

Prof. ROLLINS emphasised that apomicts do exist in nature.

Mr. ROSS considered this to be an amendment consequential on later proposals. Therefore leave it to the Editorial Committee to include or leave out according to our acceptance or not of these later proposals of Dr. CAMP.

After this there was some discussion as to whether apomicts were taxa or not, several members took part, amongst them Profs. ROBYNS, ROLLINS and LANJOUW.

Prof. MATTFELD: Dieser Vorschlag ist wesentlich systematisch und nicht nomenklatorisch; er gehört daher eigentlich nicht in die Nomenklaturregeln hinein. Die Forschung kann so viele Kategorien bilden, wie sie benötigt; Aufgabe der Nomenklaturregeln ist es dann nur, für den allgemeinen Sprachgebrauch den Rang dieser Kategorien im hierarchischen System der Kategorienwerte festzulegen!

Der Terminus "apomict" hat überhaupt keinen Kategorienwert; es gibt apomiktische Familien, Gattungen, Arten und infraspezifische Taxa; bei *Hieracium* gibt es apomiktische und amphimiktische Blüten in demselben Köpfchen und bei *Rubus* apomiktische und amphimiktische Eizellen in derselben Blüte!

Der Begriff Population und andere im Zusammenhang mit genetischen Analysen geschaffene Begriffe wie Ökotypus, Ökospecies, Coenospecies, Commiscuum, Comparium, Convivium und ähnliche haben ihre besondere Bedeutung für sich; sie stimmen aber mit den taxonomischen Kategorienwerten nicht oder nur in Einzelfällen überein; auf keinen Fall können sie die letzteren ersetzen!

Prof. ROLLINS said many morphologically distinctive populations of plants existing in nature and reproducing by apomixis are now being described in many genera as species, using the binomial for them. These populations of plants are often called apomicts—it seems important to provide a nomenclatural category for these plants, for their description as species

is unnecessarily burdening our nomenclature and subverting the usual species concept.

Dr. FOSBERG suggested that Prof. ROLLINS was considering population behaviour as the only criterion of species but that morphology still remains the means of identification of these taxa. It still seemed that an apomict might be morphologically a species, variety or form or other category of taxon.

Dr. HYLANDER again suggested that a note should be appended to the present Article explaining that such concepts as apomicts are dealt with in another chapter.

Dr. RAMSBOTTOM emphasized the difficulty of dealing with apomicts, but considered that we must try and include them in a sensible form in our Nomenclature; after all they are plants!

Prof. MARTIN said that the last sentence of Article 12 provided for the use of special categories as needed.

Dr. SPRAGUE supported the view of Dr. HYLANDER and proposed "*For categories specially applicable to the genetic analyses of taxa see Art. 34 ter, 34 quater, 35 quinquies.*"

Dr. HYLANDER seconded this.

Prof. MERRILL read out Dr. SPRAGUE's proposal to be voted upon.

This was translated by Prof. ROBYNS and Prof. MATTFELD into French and German.

There was then a vote by show of cards and it was carried unanimously.

PROP. 8 (4: 204) Rejected

Recommendation II

PROP. 1 (65: 110) Rejected.
PROP. 2 (186: 45) Accepted.
PROP. 3 (44: 141) Rejected.

New Recommendation II bis

PROP. (81: 135) Withdrawn.

A short discussion took place on the term "*grex*". The following took part: Prof. LANJOUW,

Dr. ROGERS, Prof. PAPPENFUSS, Dr. HYLANDER, Dr. SPRAGUE, and Dr. DONK.

Prof. LANJOUW wished to withdraw New Rec. II bis explaining that he had merely tried to find a place for "*grex*," which has been used in a different sense by various authors.

Dr. ROGERS said that Dr. BRIQUET pointed out in the "Proceedings" of an earlier Congress that "*grex*" had been used in so many senses that it had no meaning of its own. He therefore recommended that it be not included in the series of acceptable categories, and this was followed by that Congress.

Dr. DONK moved to amend the proposal in the following manner: Due to the different uses of the term "*grex*" its use should be discontinued.

Prof. MATTFELD: Es ist dringend davon abzuraten, das Taxon "*grex*" als neue Kategorie zwischen Species und Subspecies einzuführen. Meines Wissens ist der Terminus *grex* bisher nur als intragenerische Einheit, ähnlich dem Terminus *series*, für Artgruppen benutzt worden; vgl. z. B. ENGLER et IRMSCHER, *Saxifraga*, in ENGLER, Das Pflanzenreich IV, 117 I (Heft 67) 1916, p. 6 etc. Alle mit dem Zeichen § versehenen Taxa ENGLERS (und vieler anderer Autoren) sind *greges*!

Würde diese neue Empfehlung und zugleich auch Art. 13 Prop. 1 angenommen werden, dann würden alle bisherigen *greges*-Namen illegitim werden. Daher kann ich weder dieser neuen Empfehlung noch dem Art. 13. Prop 1 zustimmen.

Dr. SPRAGUE said that the term "*grex*" had been used by KOEHNE (Engl. Jahrb., vol. 1, p. 455) for a category between subgenus and section, and was now proposed by Dr. CAMP (Art. 34, Prop. 5) for a group of hybrids of the same parentage but differing in morphological characters. He suggested that the term be excluded from the main body of the Rules, and be left to Dr. CAMP to employ as he liked in his Supplement to the nomenclature of hybrids.

Prof. LANJOUW withdrew Rec. II bis, and it was decided accordingly that the term "*grex*" be not included in the accepted categories.

SESSION 3

July 8th, 10 a. m. — 12.35 p. m.

Chairman: T. A. SPRAGUE

Dr. SPRAGUE first spoke of the importance of speeding up the work and urged that matters of small importance should not be given undue time in discussion. Judging from the time we had taken so far we should need eighteen days to complete the discussion.

This was followed by a statement from Prof. LANJOUW as Rapporteur, on the distribution of votes, he explained how votes were allotted by the Organising Committees at Cambridge, Amsterdam and Stockholm to Botanical Institutions, Societies and Academies and that there was no cut and dried system. Anyone who felt that his or her Institution etc., had been granted too few or too many votes should inform the Rapporteur and the matter would be looked into before the next Congress.

The Swedish Organising Committee made a first list which was submitted to the Rapporteur, who suggested certain minor changes. Proposers of motions were allotted one vote, irrespective of the number of their proposals. Members of one or more Nomenclatural Committees had one vote, and officers of the Bureau one vote, the maximum number of personal votes thus being three.

Article 13

PROP. 1 (206: 45)

Dr. SPRAGUE wished to modify his proposal by substituting the words "belonging to" for "placed in."

Dr. ROGERS proposed the following addition to Prop. 1:

"An exception is made for names of subgenera in FRIES's *Systema Mycologicum*, which are treated as validly published although he termed them "tribes" (tribus).

Prof. MATTFELD: Das Beispiel *Delphinium* tribus *Involuta* Huth etc. ist bisher so gelöst worden, dass man die Namen Huth's angenommen und, ohne das Autorensitzat zu ändern, HUTH's *tribus* = *series* oder *grex* Autorum gesetzt hat. So ist z. B. ENGLER schon 2 Jahre nach dem Erscheinen von HUTH's Monographie verfahren: ENGLER in ENGLER und PRANTL, Die natürlichen Pflanzenfamilien, Nachtrag 2 zu Teil II-IV, 1897, p. 168: *Delphinium* subgen. I. *Consolida* DC. § 1 *Involuta* Huth, § 2 *Brevipedunculata* Huth; subgen. II. *Eudelphinium* Huth, sect. I. *Elatopsis* Huth, § 1 *Brevicalcarata* Huth. Ebenso verfährt auch GRAEBNER in ASCHERSON und GRAEBNER, Synopsis der Mitteleuropäischen Flora, V 2, 1929, p. 662 ff. HUTH's Namen sind allgemein anerkannt, und man kann sie jetzt nicht einfach für nicht gültig veröffentlicht erklären!

Art. 13 besagt, dass "a genus containing tribes is inadmissible." Daraus geht aber nicht hervor, dass die Namen dieser Taxa geändert werden müssen oder können. Die einfachste Lösung dieser Frage scheint mir daher die zu sein, dass nicht die Namen der Taxa für nicht gültig veröffentlicht erklärt werden, sondern dass statt der falsch verwendeten Kategorien-Termini die richtigen Termini eingesetzt werden. (In diesem Sinne wird in einem ähnlichen Falle ja auch in Art. 24 Prop. 4 p. 53 entschieden. Vgl. auch die Erörterungen von FURTADO auf p. 32 oben.)

Ich schlage vor, dem Art. 13 folgenden Passus hinzuzufügen: "Werden die Namen solcher Taxa später benutzt, so hat man ihnen den ihrer Rangstufe zukommenden Kategorienterminus zu verleihen; dies hat keine Änderung der Autorschaft zur Folge."

I propose to add to Art. 23 the following

sentence: "Who uses the names of such taxa, must give them the right terminus of the proper category; this does not involve change of authorship."

Add to the example: ENGLER (in ENGLER und PRANTL, *Die Natürlichen Pflanzenfamilien*, Nachtrag 2 zu Teil II-IV, 1897, p. 168) changed the terminus *tribus* of HUTH in § (id est = *series* = *grex*).

Dr. FOSBERG said that the tribes of FRIES, when changed to their proper rank will be automatically validated when taken up and typified by reference to FRIES's descriptions.

Descriptions do not have to be validly published to be used as the basis of names.

Dr. SPRAGUE suggested that this be referred to the Mycological Committee.

Prof. SINGER said that since there was an amendment to Prop. 1, the mycologists might consider to drop their own proposal and accept the amended proposal.

Dr. SPRAGUE agreed to accept this if the Mycologists were satisfied.

Dr. RAMSBOTTOM thought it should be considered by the Mycological Committee.

Dr. ROGERS promised to call a meeting.

Dr. SPRAGUE suggested that he should report the result on the following Monday or Tuesday.

Article 14

- PROP. 1 (187: 48)
 PROP. 2 (4: 210)
 PROP. 3 (17: 185) Withdrawn.
 PROP. 4 (4: 209)
 PROP. 5 (49: 163)
 PROP. 6 (26: 172)

Dr. CAMP suggested that Prop. 1 be accepted.

PROP. 1 (LANJOUW)—Delete the Article and replace it by the following note at the end of Chapter II: "The definition and nomenclature of categories such as hybrids, artificial polyploids, chimaeras, etc. are dealt with in § 6".

Dr. SPRAGUE put Art. 14, Prop. 1 to the vote by show of cards.

Carried by a large majority.

Chapter III Names of taxonomic groups

- PROP. 1 (14: 209) Rejected.

Article 15

- PROP. 1 (9: 227) Rejected.

Article 16

- PROP. 1 (8: 214) Rejected.

- PROP. 2 (192: 32) *Accepted.*

- PROP. 3 (70: 76)

Dr. SPRAGUE suggested that Prop. 3 should be referred to the Editorial Committee.

Vote by show of cards *confirmed this.*

- PROP. 4 (14: 216)

Dr. HYLANDER said the article was withdrawn except the lines "An epithet is not considered illegitimate only because it was originally published under an illegitimate generic name, but must be taken into consideration for purposes of priority if the epithet and the respective combination are in other respects in accordance with the Rules. In the same way, an epithet of a subspecies of a taxon of a lower rank may be legitimate even if originally published under an illegitimate name of the subsequent higher taxon."

Dr. FOSBERG said that there was no doubt that the statement regarding illegitimacy in Art. 60 was ambiguous and needed clarification. Therefore he moved that the Editorial Committee be instructed to place a note embodying the two sentences of Dr. HYLANDER's Prop. 4 as given above.

Dr. DONK said that specific names of the binomial system of nomenclature have their right of standing thanks to two descriptions, a generic one and a specific one; if one of these is not validly published the whole specific name ought to be considered as not validly published. He said he would like to have it on record that if "illegitimate" in Dr. HYLANDER's proposal also would cover "not validly published" the proposal was not acceptable as it now stood.

It was proposed by Dr. FOSBERG and seconded by Prof. ROLLINS that *these two sentences of Dr. HYLANDER's proposal be submitted to the Editorial Committee for insertion with proper wording.*

Dr. SPRAGUE then put Dr. FOSBERG's motion to the vote.

This vote by show of cards resulted in the proposal being accepted by a large majority.

A few remarks were then made on Art. 16 Prop. 3 by the Japanese Botanists, which had already been referred to the Editorial Committee. Dr. SPRAGUE told Dr. NAKAI that he thought the word "taxonomic" might be better than "systematic," but the Editorial Committee was authorised to consider this.

PROP. 5 (87: 68)

Prof. LANJOUW explained the proposal of Dr. WEATHERBY and said that if the proposals mentioned by Dr. WEATHERBY were agreed upon, this proposal too would have to be accepted, although possibly with amendments.

Dr. ROSS thought that since, if we accept Art. 26 bis and Art. 28 bis, which are the alternative methods of dealing with this proposal, to those mentioned in the proposal, or if we accept the proposals mentioned, they become part of the Rules and these exceptions are unnecessary.

It was proposed by Prof. LANJOUW and seconded by Dr. FOSBERG that *this be sent to the Editorial Committee.*

Dr. SPRAGUE put this to the vote by show of cards and it was carried.

PROP. 6 (77: 60)

The discussion on this proposal was postponed till Rec. VIII, Prop. 4 was considered.

Article 17

PROP. 1 (7: 237) Rejected.

PROP. 2 (30: 214) Rejected.

Recommendation III

"Changes in nomenclature should be made only after adequate taxonomic study."

Although there were no proposals sent in concerning this Recommendation there was some discussion on the Recommendation.

Le Prof. BAEHNI propose de transformer cette recommandation en une Règle. Il cite l'exemple d'un archiviste (O. SCHWARTZ in Ber. Thür. Bot. Ges.) qui, par de simples recherches bibliographiques, a publié un grand nombre de modifications de nomenclature sans avoir même regardé les spécimens d'herbier. Il trouve qu'il s'agit là d'un travail d'archiviste et non de taxonomiste.

Prof. LANJOUW agreed with Prof. BAEHNI, but said that it would be difficult to use this recommendation, we should need a Supreme Court to refer to for certain decisions. He thought Dr. BRIQUET made this a Recommendation rather than an Article because he saw the difficulty of enforcing it.

Dr. LE GAL apporte l'accord des mycologues français à la Proposition du Prof. BAEHNI.

Dr. DE WIT said a "black list" of works, not admitted for nomenclature purposes, might have the result that many publications containing new names or changes of names made after inadequate *systematic* study would be outlawed and thus cease to be a burden to nomenclature.

Many works were not written for nomenclatural or systematic purposes but contained new names, unidentifiable but no "nomina nuda." By "black-listing" works for *nomenclatural purposes* much discussion and trouble would be avoided. He added that the action of the French botanists also leads to this "black list."

Prof. LANJOUW agreed, but said that already there was a Committee appointed for that purpose, but it was practically impossible to come to satisfactory conclusions on certain works brought up for consideration. Still more so would it be difficult to act on Prof. BAEHNI's proposal.

Dr. FOSBERG said that if the Recommendation were made a Rule it would be retroactive.

Prof. SINGER suggested that a possibility for an adequate wording of the Recommendation if it should be voted to be a Rule might be

"Nomenclatural changes in other than comprehensive treatments shall be made only in or as a result of a systematic study."

Dr. BOIVIN said it would rule out O. KUNTZE's names.

Prof. BAEHNI then said the rule should not be retroactive and there should not be a "black list" of works. Draw the line by making it monographic revisions or partial monographic revisions.

Dr. SPRAGUE asked Prof. BAEHNI if he meant that changes were to be made only in Monographs and Revisions.

Prof. BAEHNI: Yes.

Mr. ALSTON suggested that the proposal would rule out such a work as CHRISTENSEN's *Index Filicum*, where a very large number of new combinations were made, which were based on a study of the literature rather than the plants. Most of these names he said were still in common use.

Dr. PATRICK considered it should remain a recommendation. We could only recommend that people make nomenclatural changes only in monographs or in serious taxonomic work—we cannot legislate. The special committee should consider and if necessary make proposals to deal with such nomenclatural changes if they are inadvisable.

Le Prof. HOCHREUTNER se demande quelle raison il peut y avoir de refuser la transformation de la Recommendation III en Règle si l'on accepte l'Art. 17?

Le Prof. HUMBERT signale que la question est très sérieuse. Il s'agit, en effet, de savoir si un archiviste, ou un bibliothécaire peut, sans même connaître les plantes dont il a relevé les noms dans une publication, imposer son point de vue aux taxonomistes.

Dr. ROGERS said that Art. 17 allows change because of the "necessity of giving up a nomenclature contrary to the Rules." Rec. III, if an Article, would forbid change except "after adequate taxonomic study" and would prevent the rectification of illegitimate nomenclature.

Dr. SPRAGUE said that Recommendation III seemed to be almost superfluous.

Prof. LANJOUW suggested that perhaps it would be as well to delete Art. 17 and Rec. III.

Dr. A. C. SMITH wished to keep in the Rules both Art. 17 and Rec. III as they stand.

Dr. RAMSBOTTOM supported this. He said Rec. III could not be made an Article unless there were a supreme authority to make decisions.

Dr. DONK proposed to substitute the present Art. 17 by Prop. 1 of FURTADO and to leave Rec. III as it stands. In the proposal cited he said that every reference "to adequate taxonomic study" is left out. This changed Article would be supplemented by the Recommendation perhaps precisely in the manner wanted by a large part of those present.

Dr. RAMSBOTTOM asked for a vote on Dr. SMITH's proposal to leave Art. 17 and Rec. III as they stand.

Dr. SPRAGUE first put to the vote Prof. LANJOUW's *proposal to delete Art. 17*.

This was *rejected* by a show of cards.

Dr. SPRAGUE then said he thought last minute proposals ought to be given time for consideration.

Dr. A. C. SMITH again suggested that a vote should now be taken on *leaving Art. 17 and Rec. III precisely as the stand*.

Dr. SPRAGUE put this motion to the meeting and by show of cards it was *carried* by a large majority.

Leave Art. 17 and Rec. III as they stand.

Section 2. The type method

Prof. LANJOUW explained to the meeting that a Committee had been set up to consider the Type method and to consider the various proposals set out under Art. 18 and he suggested that discussion on the Type method had better be postponed till we receive a report from that Committee.

Dr. RAMSBOTTOM agreed.

Dr. CAMP asked whether it would be possible to have a mimeographed copy of the findings of the Committee.

Prof. LANJOUW thought that would be possible.

He then read the names of the Committee members so far, and asked if there were any others.

Dr. RAMSBOTTOM suggested the Secretaries of the various committees. Others suggested were Mr. AIRY SHAW and Dr. ROGERS.

Dr. FOSBERG suggested a meeting of the Committee as it stood should be held that day in order to co-opt members ready for the full meeting the next day.

This was agreed.

Section 3

PROP. 1 (1: 215) Rejected.

Article 19

PROP. 1 (2: 233) Rejected.

PROP. 2 (23: 201) Rejected.

New Article 19 bis

PROP. (1: 235) Rejected.

Article 20

PROP. 1 (47: 34)

Dr. SPRAGUE said that this was for the Diatom Committee to report.

Mr. ROSS said that the Special Committee for Diatoms voted as follows:

Against the proposal: 7.

For the proposal: 2.

In favour of 1844 as starting date: 1.

Afterwards there appeared to be a general consensus of opinion against the proposal.

Mr. ROSS considered that this view should be accepted by the Congress.

Dr. RUTH PATRICK *withdrew the proposal*.

PROP. 2 (3: 212) Rejected.

PROP. 3 (172: 46)

Dr. SPRAGUE asked Dr. RAMSBOTTOM if he would care to speak.

Dr. RAMSBOTTOM said he would prefer to wait until the Mycological Committee had reported.

Prof. LANJOUW said he thought this referred to other groups as well as Mycology.

Dr. RAMSBOTTOM said he thought the starting point should be *definite*, the date of the years alone he considered as not enough.

Mr. DANDY said that although at first he supported this proposal he now thought that it required further consideration. He said that, as Prof. LANJOUW had pointed out, it concerns other groups besides Cryptogamy. For instance LINNAEUS's *Demonstrationes Plantarum* published in 1753 after the *Species Plantarum*, contains new specific names of Flowering Plants, which, if this proposal were adopted would be deemed as not published.

Dr. SPRAGUE said he considered that was a very important point.

Dr. BLAKE suggested that it might be Jan. 1st in all cases.

Prof. ROUSSEAU said he thought that the meaning of the proposal is that a book chosen as the starting point is considered as having been printed on 31st December.

Dr. HYLANDER proposed to choose as printing date of Linnaeus' *Species Plantarum*, Dec. 31st 1753.

Prof. LANJOUW thought that if we choose Jan. 1st all works printed in the same year would get into sympathy. We must take either Jan. 1st or Dec. 31st.

Mr. ALSTON said he thought we ought to start with the date and not with the book.

Dr. SPRAGUE said he thought that if the Special Committee for each group decided on the date for that group, the proposal would hardly be necessary.

Prof. VAN DER WIJK said that by accepting Dec. 31st, all other works published in the year of the starting point become automatically invalid. It saves a lot of trouble, and in the case of *Musci*, removes a number of insolvable puzzles.

Prof. BAEHNI asked if this would be retroactive.

Dr. ROGERS proposed an amendment to Prop.

3; after "starting point" insert "and whose relative dates are not known."

Prof. PAPENFUSS said that someone might find a date later, so it was essential to fix the date.

Mr. ROSS said we must have either Jan. 1st or Dec. 31st as the fictitious date of publication of all starting-point works other than the *Species Plantarum* of LINNAEUS, otherwise the discovery of relative dates not now known will upset nomenclature. Which of the two dates should be left to the Special Committee concerned.

Dr. HYLANDER thought we might accept these dates in principle and add Dr. ROGER's proposal.

Dr. RAMSBOTTOM thought there must be a precise date and the question was should this be Jan. 1st or Dec. 31st.

Prof. MARTIN proposed that after "latter work" the words "unless it is clearly established that they are later" should be added.

Dr. ROGERS wished to withdraw his proposal in favour of Dr. MARTIN's.

Dr. BLAKE said if it were Jan. 1st, it must be from Jan. 1st of the next year.

Dr. SPRAGUE thought we might have a vote as to whether each group mentioned in Art. 20 should have a date, either Jan. 1st, or Dec. 31st.

Dr. FOSBERG asked if this included LINNAEUS' *Species Plantarum*.

Dr. SPRAGUE and Prof. LANJOUW said yes.

Prof. BAEHNI asked if it would be retroactive.

Dr. BOIVIN asked if it could be left open which date to use.

Dr. HYLANDER thought we could now vote on the choice of date, and then discuss *Species Plantarum*.

Dr. RAMSBOTTOM thought the *Species Plantarum* was on an entirely different footing and he proposed we should vote on all works except *Species Plantarum*.

Dr. SPRAGUE said he was prepared to have a vote on all works except *Species Plantarum*.

Prof. LAM suggested that it might be better to vote first for *Species Plantarum* Jan. 1st or Dec. 31st.

Prof. ROLLINS made an amendment to May 1st.

Dr. HYLANDER thought that if we chose May 1st there would still be much trouble.

Dr. FOSBERG thought we could not completely avoid trouble.

Dr. SPRAGUE then ruled that a vote by show of cards would be taken as to whether we should accept May 1st 1753 as the date for *Species Plantarum*.

The proposal was carried by a large majority.

A second proposal to have a conventional date (either Jan. 1st or Dec. 31st) for all other works accepted as starting-point was also carried by a large majority.

PROP. 4 (27: 28)

This was postponed until the Algologists presented their report.

PROP. 5 (64: 36)

To await Mycological Report.

PROP. 6 (33: 23)

To await Mycological Report.

PROP. 7 (33: 13)

To await Paleobotanical Report.

PROP. 8 (62: 80)

It was proposed to discuss this later.

PROP. 9 (1: 216) Rejected.

PROP. 10 (15: 161)

Dr. HYLANDER said that part of this proposal of his would be considered by the Paleobotanists. He explained what was meant by the proposal and that the important point was paragraph 3.

Dr. FOSBERG moved that the footnote to Dr. HYLANDER's proposal be added as a note to Art. 20.

Mr. ROSS said that we need to cover the standing, as earlier homonyms, of names published between 1753 and later starting points.

Dr. SPRAGUE asked Dr. FOSBERG and Mr. ROSS to get together at lunch time and draft a proposal as to what they would like to add as a footnote to Art. 20.

SESSION 4

July 8th, 2—5.30 p. m.

Chairman: T. A. SPRAGUE

Article 21

PROP. 1 (136: 69)

Prof. ROUSSEAU suggested that the first part of this proposal (i.e. note 2), be accepted, namely "The application of both conserved and rejected names is determined by nomenclatural types, or by substitute types where necessary or desirable."

It was agreed to accept of Prop. 1 note 2 in principle and refer it to the Editorial Committee. Note 3 was rejected.

PROP. 2 (3: 216) Rejected.

PROP. 3 (11: 201) Rejected.

PROP. 4 (79: 36)

This being a purely textual amendment was referred to the Editorial Committee.

PROP. 5 (177: 32)

Accepted and referred to the Editorial Committee.

PROP. 6 (169: 40)

Dr. SMITH accepted Prof. LANJOUW's amendment that it is advisable to replace "families and genera" by "genera and taxa of a higher rank."

Dr. SPRAGUE put this to the vote by show of cards.

This was carried.

PROP. 7 (27: 40)

Dr. BOIVIN explained that he did not consider *Alsine* a good example.

Dr. SPRAGUE agreed and suggested that Dr. BOIVIN's proposal should be referred to the Editorial Committee. This was agreed.

PROP. 8 (16: 179) Rejected.

It was decided however, that the Editorial Committee be asked to consider the examples given by Dr. HYLANDER. It was also decided to refer to the Editorial Committee the suggestion that if conservation of a generic name proves to be unnecessary it should be withdrawn (see bottom of p. 39 Synopsis of Proposals).

PROP. 9 (25: 197)

A great deal of discussion took place concerning the advisability or otherwise of *nomina specifica conservanda*. Dr. SMITH put forward the following motion to the Congress "That this Congress is opposed to the principle of *nomina specifica conservanda* and *rejicienda*."

Dr. ROGERS gave a short account of an informal meeting (of which he was Chairman) of the Committee set up at Utrecht to consider *nomina specifica conservanda*. This was attended by only three or four actual members plus nine or ten non-members who were interested in the subject. Dr. ROGERS said that the adoption of *nomina specifica conservanda* was put to the vote and that there were no votes in favour of the motion. Then the committee was asked to vote on whether some form of *nomina specifica rejicienda* should be adopted. The voting in this case showed four in favour of the motion.

Mr. GILMOUR drew attention to an omission in Dr. ROGERS' report of the informal meeting. The "Committee" was first asked to vote on the following motion: "That some means should be adopted to permit the retention of certain illegitimate epithets," and the voting in this case was eight in favour and five against, a clear in-

dication that the Committee was in favour of the principle.

Prof. LANJOUW asked Dr. SMITH if he were also opposed to the principle of *nomina specifica rejicienda*.

Dr. SMITH said he would rather not include the question of *rejicienda*, although if Prof. LANJOUW wished it he would add it.

Dr. SPRAGUE asked Dr. SMITH to give his arguments against *nomina specifica conservanda*.

Dr. SMITH replied that the arguments should be put forward by people who wished to change the Article.

Mr. GILMOUR, in supporting the principle of *nomina specifica rejicienda*, said he believed that he was speaking on behalf of a large body of horticulturists and other non-taxonomic users of plant names who were anxious to co-operate with taxonomists, but felt that the time had come to adopt some method of avoiding changes in well-known names that had been widely used over a long period. He emphasised that he was not seeking to prevent changes due to altered taxonomic opinion, but only those due to the discovery of earlier, overlooked, synonyms and homonyms. Further he did not wish to suggest that any new rule should be retroactive; changes already accepted therefore would be unaffected.

Provided that only really well-established names of widely used economic plants were considered, he did not think the list of rejected names would be a long one. The existing list of *nomina generica conservanda* was not comparable, as the majority of these generic names were not of economic importance.

It may be argued that, as only a few names would be involved, it would not be worth while legislating to avoid changing them. It was, however, not primarily the number of names that was important, but the number of users who would be inconvenienced and annoyed by the change in any particular name. For example, if the name *Viburnum fragrans* was changed, as it should be under the existing Rules, users of references to the species in books, articles and

catalogues all over the world would be affected. Such changes undoubtedly had a very bad effect on the relations between taxonomists and other botanists, and if they continued, co-operation between the two groups would be seriously prejudiced. He therefore made a strong plea to the Section to adopt some form of *nomina specifica rejicienda* as a valuable step towards continued and improved co-operation between taxonomists and other branches of plant science.

Any step to avoid such name changes involved, of course, a suspension of the principle of priority. Such suspension, however, had already been accepted in the case of generic names, and in other Articles of the Rules, and he urged that the principle of *stability* was at least as important as the principle of priority; the latter was, indeed, only a means towards the accomplishment of the former, and if priority did not, in any particular field of nomenclature, result in stability, surely it was in accordance with the spirit and intention of the Rules, that priority should give way in the interests of the wider principle.

Mr. DAXTON of the U. S. Forest Services said that Mr. GILMOUR had intimated that the demand for conserved species names came mainly from practical workers with plants who are not unnaturally irritated by numerous changes in the names of economic plants with which they deal. He would like to call attention to the case of the largest and perhaps oldest tree in the world, the giant Sequoia (*Sequoia gigantea*, *S. Wellingtonia*, or if one followed a different generic concept *Sequoiadendron giganteum*). The U. S. National Park Service has most exclusive jurisdiction over this tree and refuses to use any other name for it than the illegitimate *Sequoia gigantea*. In a paper he published a few years ago he showed that about 75 % of Californian botanists prefer to use this same illegal name. A condition, therefore, rather than a theory, confronts us here. For his own part he was quite willing to abide by the majority of opinion of systematists in this case. If, however, the principle of *nomina specifica conservanda* is re-

jected, he hoped a committee would be re-constituted to co-operate with the International Horticultural Congress in preparing a list (much as the last International Botanical Congress approved in principle) that would be standard for, say, a period of at least ten years for the use of practical workers with plants.

Mr. STEVENSON said that American plant pathologists were much concerned with the constant name changes, and the principle of *nomina specifica rejicienda* offered a helpful way of meeting the problem.

Dr. SPRAGUE laid stress on the fact that these practical workers did not wish to make the proposals retroactive.

Mr. STEVENSON agreed.

Prof. LAM said he was opposed to both *nomina specifica conservanda* and *rejicienda*, but that he appreciated the view-point of the horticulturists. The main difficulty to him seemed to be where to draw the line.

Dr. SMITH said the impression so far given was that *all* horticulturalists were in favour of Dr. LITTLE's proposal which was not correct. He read statements from letters sent to him by two or three representatives of leading U. S. Schools of Forestry, indicating that no unanimity on the subject exists among American foresters. The opinions quoted demonstrated that at least some foresters are willing to abide by the current practices of taxonomists and that they do not favour the principle of *nomina specifica conservanda*.

Prof. LAWRENCE said that as a member of the staff of the Bailey Hortorium, Cornell University, he had been directed by his superior, Dr. L. H. BAILEY, to bring to the notice of this Congress his view that as a result of seventy years of dealing with the nomenclature of native and cultivated plants, it is now his considered opinion that the principle of *nomina specifica conservanda* is unscientific, not to be given favourable consideration and that he is unalterably opposed to it. He produced two documents—resolution in opposition to the principle of *nomina specifica conservanda* from the Executive Committee of the American

Society of Horticultural Science, and a duplicate resolution from the Commission on Nomenclature of the American Horticultural Council.

He said he was certain that he was correct in saying that the professional American horticulturists were, in the majority, opposed to the principle of *nomina specifica conservanda*.

Dr. SPRAGUE proposed the following motion, which was seconded by Prof. LANJOUW and carried with acclamation, that Prof. LAWRENCE be asked to convey to Prof. BAILEY on behalf of the Section of Nomenclature their deep appreciation of all that he had done in the field of Botany and Botanical Nomenclature, together with their regret that he was unable to be present at its sessions.

Dr. BOIVIN thought that if the principle were accepted, the number of names placed on the list would be very great.

At this stage a new proposal put forward by Dr. GLEASON was discussed for a short time.

Dr. RAMSBOTTOM brought forward the proposal given in Art. 49 ter by the Association of Applied Biologists. This suggested the rejection of specific names, not epithets.

There can be no doubt said Dr. RAMSBOTTOM that the feeling amongst practical men, i.e. those engaged in growing plants, is greatly in favour of some form of conservation of specific names or epithets.

Dr. SPRAGUE suggested the alteration of the wording in Art. 49 ter, line 6 from "illegitimate" to "not validly published."

Dr. HYLANDER thought that specific names published before 1890 and not accepted by other than their authors should be rejected.

Dr. SPRAGUE said that before 1890 some rare South American plants were found, which had not since been rediscovered, and which might therefore not have been mentioned by later authors, if no revision of the genera concerned had been published in the meantime.

Dr. FOSBERG said that most provisions in the proposals under consideration depended on matters of opinion such as general use, economic importance, etc. These are obviously imprac-

tical. Furthermore the idea that the list can be kept small is idealistic.

Judging by the experience with a list of *nomina generica conservanda*, we may not expect that this list will be kept small, as human psychology will not likely change. Further we have probably found most of the obscure books and articles that will cause trouble, with the intense activity in this line in recent years, such trouble will probably decrease in the future.

Prof. BAEHNI, when asked by Dr. SMITH what his opinion was, said that he thought Swiss botanists were opposed to the idea of *nomina specifica conservanda*.

Prof. LANJOUW said that he thought most Dutch botanists were also against it, but that Polish botanists were in favour of it (letter by Prof. PAWLOWSKI "on behalf of all Polish botanists").

Mr. DRAR said that he was entirely in favour of *nomina specifica conservanda* because it is more practical. He said he would give only one or two examples experienced during his recent visit to the Far East. In many cases he had to change the names in his lists which were drawn up according to the last edition of L. H. BAILEY, because many of the technical experts of the botanic gardens were not aware of the new names, e.g. *Delonix* against *Poinciana*, *Roystonea* against *Oreodoxa*. If the matter is to be restricted to the most important economic plants, it will not be too long, and particularly in cases of universally established names since a long time.

For specific names he said he would like to draw attention to the situation in regard to *Cymbopogon* in the Far East. Many of the cultivated species are confused simply because of the non-application of the principle of *nomina specifica conservanda*.

Dr. RODHE said the Canadian Pathological Society was against the principle of *nomina specifica conservanda*.

MISS MARY TINDALE said that on behalf of the staffs of the National Herbarium, Sydney, and the Queensland Herbarium, Brisbane, she

had been asked to state that they were strongly opposed to the principle of *nomina specifica conservanda*.

Dr. ALLAN said that New Zealand horticulturalists and foresters in general support the plea for *nomina specifica conservanda* or for *nomina specifica excludenda*, to apply to plants of considerable economic importance. The difficulty of keeping such a list within reasonably small limits is recognised. Taxonomic botanists are for the most part opposed to the principle.

Mr. W. T. STEARN spoke in favour of *nomina specifica excludenda* from the standpoint of a botanical librarian and bibliographer with special reference to changes in nomenclature brought about by the rejection of later homonyms when the earlier homonym was and had been from the start a superfluous name. There are probably two thousand such names published by SALISBURY in his *Prodromus* and elsewhere which have never been used and never can be used. Some of these have necessitated the rejection of later names. Other changes from which no one will benefit and by which many will be inconvenienced must likewise be made unless the principle of *nomina specifica excludenda* is accepted. A name is primarily a key which unlocks the store of information accumulated by research during the last hundred or so years. Any change in nomenclature, whether made for good reasons or bad, renders less accessible the information recorded under the rejected name. The magnitude of the harm to botanical literature in this way has yet to be appreciated. Thus all the information about *Viburnum fragrans* Bunge, a well-known plant widely cultivated, has been recorded under this name since its publication in 1832; this name has never been challenged but is invalid; rejection of the earlier homonym would be to the good of all, as otherwise the species has to be given a new name, which in fact would be an infringement of the principle of priority. There is a real need for a means of preventing this; *nomina specifica excludenda* would do it. Any regulation should neverthe-

less be associated with certain conditions keeping a list of such names to a minimum. For example the name to be protected should apply to a plant which is cultivated and of economic importance in at least two continents; moreover this name should have been in unchallenged use in botanical literature over a long period, say a hundred years. The rejection of *nomina specifica excludenda* as a means of saving such names will probably be regretted later and the speaker urged that before it is too late this proposal should receive serious consideration.

Prof. MATTFELD: *Nomina specifica conservanda* sind ganz unerwünscht. In Deutschland sind nur einige wenige Phytosoziologen und Praktiker für eine solche Liste. Die deutschen Systematiker lehnen eine Liste der *nomina specifica conservanda* einmütig ab. — Es wird nicht möglich sein, prägnante Principien zu finden, die die Beschränkung der zu konservierenden Artnamen auf eine kleine Zahl wirklich ermöglichen. Und wenn es wirklich gelingen würde, die Zahl zu beschränken, so kann ebensogut erwartet werden, dass die Praktiker sich an diese wenigen neuen Namen gewöhnen können. Die am meisten bekämpften neuen Namen *Picea Abies*, *Quercus petraea*, *Triticum aestivum* haben sich gerade durch diesen Streit überraschend schnell in die Literatur eingeführt! Gerade den Praktikern, die es ja immer nur mit verhältnismässig wenigen Arten zu tun haben, kann man schon zumuten, dass sie den einen oder anderen dieser Namen umlernen.

Die Industrie wird durch Änderung einiger Artnamen in keiner Weise gefährdet, denn gehandelt werden die Pflanzen ja gewöhnlich unter Vernakularnamen oder unter den Namen ihrer Rohprodukte. Die pharmazeutische Industrie wird ja doch sogar dann mit den richtigen Drogen versorgt, wenn die Stammpflanze noch gar nicht benannt oder systematisch noch nicht geklärt ist! — Eröffnet man eine Liste der *nomina specifica conservanda*, so wird eine grössere Zahl von Botanikern der Nachprüfung der fortlaufend neu vorgeschlagenen Namen

sehr viel Zeit opfern müssen, die sie wirklich besser verwenden können!

Prof. ROBYS said the Belgian botanists were also opposed to it.

Mr. DANDY said he was a British botanist who was opposed to the principle of *nomina specifica conservanda*. But he was now speaking on behalf of the Portuguese botanists of Coimbra — The Instituto Botanico of Coimbra and the Sociedade Broteriana — who had asked him to oppose most strongly the principle of *nomina specifica conservanda*.

Prof. HOCHREUTNER rappelle l'histoire des Congrès qui se sont occupés des questions de Nomenclature, ainsi que quelques principes fondamentaux. Pour éviter des changements, dit-il, on propose des listes, mais qu'arrivera-t-il s'il faut les transférer dans d'autres genres ou familles. Les *nomina specifica conservanda* sont une impossibilité pratique et il propose de voter sur la question.

Dr. FRANCO said that the Portuguese botanists of Lisbon were opposed to the principle of *nomina specifica conservanda*. In his opinion, the application of the term "economic plants" cannot be equally used in all countries and that was a very important point to remember. Also he wished to recall that from LINNAEUS down to our own days there were not always the same Rules.

Dr. SPRAGUE then asked for a vote on:

"The Congress accepts the principle of *nomina specifica conservanda*."

A vote was taken by ballot with the following result:

In favour 40.

Against 320.

Majority against 280.

Dr. SPRAGUE then asked for a vote by ballot on the motion:

"That the Congress accepts the principle of *nomina specifica excludenda (rejicienda)*," with the following result:

In favour 116.

Against 242.

Dr. SPRAGUE then asked Mr. GILMOUR whether he wished to make any further state-

ment, to which Mr. GILMOUR replied that in view of the decisive nature of the voting he did not think this would serve any useful purpose.¹

Dr. SPRAGUE then said that Dr. FOSBERG, Dr. HYLANDER and Mr. ROSS had prepared their new wording of Art. 20, Prop. 10, footnote, and this was read by Mr. ROSS as follows:

"For purposes of homonymy, names in all groups validly published on or after May 1st, 1753, must be considered. Names from earlier works used in works taken as nomenclatural starting points in a sense other than that of the original author are not to be regarded as later homonyms."

Dr. SPRAGUE thought that it was unnecessary to include the date May 1st 1753, since names published before that date had no status in botanical nomenclature.

Similarly it appeared to be unnecessary to include the second sentence. He pointed out that the first sentence of Art. 20 should read: "*Valid publication of botanical nomenclature*

begins for the different groups of plants at the following dates" instead of "*Legitimate botanical nomenclature etc.*"

Mr. DANDY agreed.

Dr. FOSBERG said that if the change from "legitimate botanical nomenclature" to "valid publication of botanical names" is made in Art. 20, most of the trouble will disappear. The difficulty remaining will involve those taxa published in one group and later transferred to another with a different starting date, or a group published as a fossil and later discovered to be living, giving it a different starting date.

Dr. BLAKE thought it might be "Botanical nomenclature begins."

Dr. SPRAGUE disagreed, as botanical nomenclature was in use in the Middle Ages.

Mr. ROSS said he was prepared to accept Dr. SPRAGUE's amendment.

Dr. SPRAGUE then read out the amended version "*For purposes of homonymy, validly published names in all groups must be considered.*"

It was then decided that examples should be given and that all special committees should consider the amended version and submit their own examples to the Editorial Committee.

¹ In the final session a "Committee to deal with urgent Nomenclatural Needs" was established, especially to report on a possible solution of this problem.

SESSION 5

July 10th, 9.30 a. m. — 12.30 p. m.

Chairman: E. D. MERRILL

Dr. CAMP moved that where preliminary votings on proposals had a 2/3rds majority or more against them they should be automatically rejected unless the proposer specially wished to speak on them.

This motion was *carried* unanimously.

Prof. MERRILL then asked Dr. CAMP to give his report on the Special Committee for names of hybrid plants.

Dr. CAMP spoke of the Committee and informed the meeting that he considered it to be

very well chosen containing a good cross-section of practical workers and systematic botanists. He said they wished to replace the title of § 6 "Names of hybrids and some other special categories." He praised the work of Dr. HYLANDER both in connection with his proposals and as a member of the Committee. Dr. CAMP hoped that when the report was presented it would be accepted by the Congress.

The following are some of the proposals that would be suggested:

Modification of Art. 31, Prop. 7; Art. 31 bis; Art. 32, Prop. 6; Art. 33, Prop. 4.

New Art. 33 bis to be transferred to the new draft of Appendix VII.

Rec. XX, Prop. 1, to be deleted.

Art. 34, Prop. 4 and Prop. 5 to be combined.

New Art. 34 ter, quater, quinquies—rejected by the Committee in favour of a separate Article, to read: "Taxa which are apomicts, may be designated, if so desired, in the following manner:

1. If they are considered to be of specific rank, by the interpolation of the abbreviation "ap" between the generic name and the epithet.

2. If they are considered to be of infraspecific rank by the interpolation of the abbreviation "ap" between the category rank and the specific epithet.

Taxa which are clones may be indicated if so desired by the abbreviation Cl. or the symbol CL.

New Recommendation to follow Art. 34.

Prof. MERRILL asked if there were any questions.

Prof. HOCHREUTNER demande qu'on évite ces complications, en particulier toutes ces abréviations: *ap. cl.* etc. En effet, dit-il, nous n'avons pas de règle qui spécifie que le mot "espèce" doit être abrégé en *sp.* et que "sous-espèce" doit être abrégé en *ssp.* Il semble donc inutile d'entrer dans ces abréviations.

Dr. HYLANDER said that the intercalation of the abbreviations "*ap.*" or "*cl.*" did not affect the nomenclatural status of the names in question.

Dr. DE WIT said that the new Article stated expressly "if so desired." One is free to apply the new designations "*ap.*" etc., or not. The wishes of horticulturalists have to be recognised, and to be met as far as possible. It ought to be clearly stated whether "*ap.*" glabrum is nomenclaturally a unit (a fixed combination), or not, in cases of necessary transfers or changes.

Prof. ROUSSEAU said that all Rules must be compulsory, if not we must place the suggestion or the possibility as a note under a Rule.

Dr. RAMSBOTTOM said that additional signs

of origin in no way interfered with the usual taxonomic procedure, but were merely a method of indicating units recognisable in experimental taxonomy.

Dr. ROGERS said that we were urged to accept the category or term apomict on the grounds that it would reduce the number of binomials. The Rule or Recommendation proposed does not reduce the number of binomials, trinomials or what not. It merely requires or permits the insertion of an abbreviation.

Dr. CAMP said that he had no idea that this proposal would cause such a tempest and that he was quite prepared to make it a Recommendation rather than a Rule.

Dr. RAMSBOTTOM said that in herbaria we did not as a rule concern ourselves with apomicts, but here we had a definite group of horticulturalists who recognised them, and he saw no reason why they should not do so—there was no need to put "apomict" on a herbarium sheet.

Prof. ROBYNS said that he thought as it was subsidiary information it was better to put it in a Recommendation rather than an Rule.

Prof. HUMBERT signale que si on introduit dans les noms spécifiques, sous-spécifiques et variétaux des indications relatives à l'origine trouvée, ou supposée, de ces taxa, il n'y a pas de raison pour s'arrêter là. On pourra écrire:

Lavendula officinalis L. ssp. geogr. *pyrenaica*.

Chelidonium majus L. ssp. mutation *laciniatum*.

Trifolium repens L. fa. *altitudinis alpinum* etc.

L'objection formulée au sujet du signe relatif aux hybrides ne tient pas, car là il s'agit simplement d'un signe à placer entre les noms des plantes. Le nom d'un taxon doit être une étiquette destinée à le désigner et rien de plus; il ne doit pas inclure une dissertation, même résumée, en un mot abrégé:

La Nomenclature ne doit pas être confondue avec taxonomie.

Madame LE GAL fait remarquer que les mycologues français souhaitent que les règles de la Nomenclature soient aussi simples et peu com-

pliquées que possible, afin qu'on puisse mieux les appliquer. Elle appuie donc les remarques faites par MM. HOCHREUTNER et HUMBERT.

Le Prof. ROBYNS signale que l'intercalation des adjectifs en question ne peut être admise en principe, parce qu'il s'agit de questions de taxonomie et non plus de nomenclature. De plus, leur application rendrait notre nomenclature trinomiale.

Mr. DANDY in reply to the remarks of Prof. ROBYNS and Prof. HUMBERT said that the Rules already lay down that the origin of hybrid groups shall be indicated by the introduction of the hybrid sign. If signs such as "ap." are excluded, then the hybrid sign should be excluded also. He wished to stress again that the introduction of these signs "ap." etc. would in no way interfere with existing nomenclature. No new combinations or transfers would be required.

Dr. CAMP said they introduced this solely to clarify the position — if the Section wanted chaos, they could have chaos.

Prof. LANJOUW suggested that the whole of the Rules concerning hybrids should be placed in an Appendix at the end of the Rules.

Dr. FOSBERG said that moving this material around in the Rules made no difference, nor would it fool anyone.

If we start to include this sort of descriptive information in the names of plants, material that should be included in the description, where shall we stop?

This Section should not allow threats of formation of other rules by other groups of workers to influence our decisions. If they should form such a code they would probably have as much trouble as we have had, and would doubtless have their own special kind of chaos.

Dr. RAMSBOTTOM said there was no question of threats. The information is there. It is essential to provide some method in the Rules for those wishing to indicate it in botanical nomenclature.

Dr. SPRAGUE said he thought the whole discussion was really a storm in a tea-cup. The

Rules already provided for the giving of supplementary information. He gave the example of *Loranthus* (Sect. *Ischnanthus*) *gabonensis*, where there was special information in parentheses. He could not see any reason why such information should not be given in the case of apomicts.

The meeting signified general approval.

Dr. SINGER said that instead of recommending the use of interpolated letters like "ap." in botanical names it would be better to adopt a recommendation to which we could all agree, for example:

"Authors should indicate in separate notes the sense in which they use specific and intra-specific epithets, i.e. whether such a taxon is considered an apomict, hybrid, geographic race, etc."

Prof. MERRILL suggested a formal vote on whether the proposal on apomicts should be included as a Rule or as a Recommendation.

Prof. LANJOUW suggested a vote on the whole of § 6.

Dr. CAMP suggested a vote on the whole with the proposal on apomicts as a Recommendation.

Prof. BREMEKAMP suggested that a vote be taken that the whole of § 6 be placed in a special Supplement.

Prof. MERRILL considered that that would complicate the issue. He called for a formal vote on the whole with the proposal dealing with apomicts as a Recommendation. A vote by ballot was taken with the following result:

In favour 284.

Against 49.

At this point the meeting was suspended for Dr. HEMMING to speak to the Section on Zoological Nomenclature. He said that he was greatly impressed by the method of procedure adopted by the botanists. He warmly approved of the Synopsis of Proposals, and said that if funds allowed the zoologists would have one next time. He gave a short account of the Zoological Rules and the various difficulties that had been encountered from time to time and drew certain comparisons between Botanical and Zoological Nomenclature.

Prof. BREMEKAMP suggested that § 6 of the Rules should be transferred to a special Supplement.

Prof. BAEHNI suggested that there might be a better title for § 6. He did not like "some other special categories."

Dr. RAMSBOTTOM suggested the omission of the word "other"; the title to read "Names of hybrids and some special categories."

Prof. MERRILL asked Dr. CAMP if he approved.

Dr. CAMP raised no objection.

Prof. MERRILL proposed that that be considered by the Editorial Committee.

Mr. DANDY and Prof. LAM thought the § 6 might remain in the Rules.

Prof. BREMEKAMP maintained his desire for a special Supplement.

Prof. LANJOUW thought that the term "Supplement" would be better than "Appendix."

Prof. MERRILL called for a vote by show of cards whether the § 6 be a Supplement.

The motion was carried by a large majority.

Dr. DE WIT requested that the Editorial Committee should consider whether "ap." and "cl." and the like should be printed in italics or not.

Prof. MERRILL said that that would be the normal procedure.

Prof. LANJOUW then read out a proposal by Mr. W. T. STEARN as an addition to Art. 20: "A name of which the publication is earlier than the starting date of nomenclature for the group to which the taxon concerned belongs, has no standing in botanical nomenclature unless re-established at or after the starting date of nomenclature for the group."

The consideration of this proposal was deferred pending the report of the Special Committee.

New Article 21 bis

PROP. (1: 237) Rejected.

New Article 21 ter

PROP. (21: 144) Rejected.

New article 21 quater

PROP. (9: 160) Rejected.

New Article 21 quinques

PROP. (29: 137) Rejected.

New Article 21 sexies

PROP. (53: 115)

Prof. LANJOUW said that although this proposal of Dr. HYLANDER had been rejected in the preliminary voting, the list of orders might nevertheless prove useful in dealing with the conservation of names of orders. He thought that that question might be considered later.

Article 22

PROP. 1 (107: 59) Accepted.

New Article 22 bis

PROP. (8: 203) Rejected.

Section 4. Nomenclature of the taxonomic groups according to their categories

PROP. 1 (10: 183) Rejected.

Prof. MATTFELD: Die Kategorienwerte der Taxa oberhalb der Ordines sind noch wenig gesichert; sie ändern sich noch ständig. Daher sollten die Namen noch nicht durch zu genaue Vorschriften in ein starres Schema gepresst werden. Eine Festsetzung der Rangordnung der Endungen dürfte genügen. Die Endung *-bionta* und die Kategorie *phylum* sind noch zu wenig und zu verschieden gebraucht, um schon in die Nomenklaturregeln aufgenommen zu werden. W. ZIMMERMANN teilt z. B. die Organismenwelt in *Anucleobionta* (= *Schizophyta*) und *Nucleobionta* und die letzteren erst in *Regnum animale* und *vegetabile*. ROTHMALER dagegen teilt offenbar umgekehrt das *Regnum vegetabile* in *Anucleobionta* und *Nucleobionta*. In diesen beiden Fällen wird also die Endung *-bionta* für Taxa verschiedenen Kategorienwertes benutzt, so dass ihre Aufnahme in die Nomenklaturregeln noch nicht empfohlen werden kann.

PROP. 2	(0: 191)	Rejected.
PROP. 3	(19: 172)	Rejected.
PROP. 4	(137: 78)	

A lengthy discussion took place on Rec. VIII, Prop. 4.

Prof. LAM said his proposals for the endings of names of taxa above the rank of family were composed after he had been requested to do so. A committee of four including Prof. LAM, Dr. RICKETT and two others, considered the proposed endings. Two were in favour and two against them. Dr. RICKETT had opposed the ending "*opsida*" and preferred "*opsea*" on philological grounds.

Dr. RICKETT thought that the proposed arbitrary endings were confusing and that "*phyta*" in particular was misleading: "*phyta*" means "plants" and it is arguable whether *Myxomycetes* are plants. A rational system is proposed as an alternative, namely to append to the first part of each name the suffix designating its category, (*phylum*, *classis*, etc.), he considered that all names should be based on types. Other names are descriptive, involving taxonomic judgments and cannot be fixed by legislation.

Dr. FOSBERG said that the Typification Committee had considered the matter of typification of categories higher than order, and decided that the application of the type method to such higher categories was impracticable.

Prof. PAPENFUSS wholeheartedly agreed with Prof. LAM's proposal that we should adopt uniform terminations for taxa above the rank of family. This is not to be interpreted that we fix the number of phyla or by what means they shall be called, merely that we fix the terminations.

Dr. BOUVIN moved that paragraph (e) "names of taxa above the rank of family must be submitted for adoption to the Congress" be deleted, as it would complicate the work of future Congresses. He moved also that the Editors should be authorised to add, delete or substitute examples in order to bring them into line with other proposals accepted. He thought the proposal was otherwise satisfactory.

Dr. BLAKE said the ending "*idae*" is the uni-

versally recognised ending for family names in Zoology. To use the same ending for Subclasses in Botany might lead to great confusion.

Prof. MARTIN said that the rule of priority as applied to orders would be extremely difficult to apply in mycology and it would be better to make the rule apply only to taxa above the rank of family.

If this were a recommendation it would be acceptable, but not as an Article.

Dr. DONK wished to point out that in accepting this proposal, paragraph (b), you neglect the fact that at present and in the future some botanists are grouping together certain *Fungi* as well as *Algae* in one class. CLEMENT and SHEAR, "Genera of Fungi", is an example. They will not be able to follow this recommendation. A second point is that "autotrophic" as used in the proposal does not take into account the fact that there are autotrophic organisms among plants that do not possess chlorophyll, e.g. *bacteria* and heterotrophic ones that do not belong to the *Fungi*.

Dr. RAMSBOTTOM said that if some of these proposals were adopted it would put every textbook in existence out of date. Mycologists will certainly not adopt any name put forward merely to gain uniformity throughout, a uniformity for which there seems to be no practical necessity.

Dr. ROGERS predicted that whatever is done by Phanerogamists in the way of establishing names of higher categories based on type genera, the mycologists will continue to use the descriptive names *Myxomycetes*, *Phycomycetes*, *Ascomycetes* and *Basidiomycetes*, as well as others above the rank of order.

Dr. SPRAGUE thought it was undesirable to fix the names of higher taxa in the plant kingdom. When new classifications were based on the possession of a particular character it was useful to use corresponding descriptive names, such as *Monocotyledoneae* and *Dicotyledoneae*, *Polypetalae*, *Gamopetalae* and *Apetalae*. Neither the rule of priority nor the type method was applicable to such names which stood or fell with the basis of classification adopted. The

type method is at present used for names of families and taxa of lower rank, and extends also to the names of orders where these are based on names of families, e.g. *Malvales*. He proposed that the rules of priority and typification should not apply to names of taxa above the rank of order.

Dr. HYLANDER said that the systematic arrangement within most cryptogamic groups is still so far from established that it will be very difficult to create usable names for categories between divisions and orders; the rank of a certain group, (e.g. the Diatoms), is by different taxonomists judged very differently, and thus in different systems these groups will get different names.

Prof. MERRILL said there was a motion before the house and he read out Dr. SPRAGUE's proposal.

Prof. PAPENFUSS said he thought we only wanted to fix the termination now. He said we already had the ending "*phyta*" so why not adopt it.

Prof. MARTIN said that those who do not regard the fungi as plants will object to being compelled to use "*Mycophyta*" for a group which they do not regard as plants.

Prof. LAM said he was well aware of the many difficulties that existed. The origin of his proposal was the growing confusion of names of higher categories. He emphasised the desirability of having *fixed endings* only. He could not fully judge the *Thallophyta*, but he thought the method could be applied to the *Cormophyta*.

A short talk on Conservation and Typification then took place, the following taking part: Drs. SPRAGUE, RICKETT, FOSBERG, LANJOUW and BLAKE.

Prof. ROBYNS then asked if we could vote on the proposal of Dr. SPRAGUE.

Prof. MERRILL put this to the vote by show of cards and it was *carried*.

New Recommendation VIII

PROP. (19: 139)

Prof. LANJOUW proposed that *this should be deleted*, as the matter should be referred to a

permanent organisation for nomenclature and not to a Congress. The examples could be referred to the Editorial Committee. This was *agreed*.

Prof. BREMEKAMP proposed to delete paragraph (b) of Rec. VIII, Prop. 4.

Prof. LANJOUW asked that (e) should be deleted as proposed by Dr. BOIVIN.

Prof. LAM agreed and *withdrew* (e).

It was further moved that all examples should be referred to the Editorial Committee who should consult the special committees.

Prof. MERRILL then called for a *vote on the acceptance of Prof. LAM's proposal in principle with the above amendments* (deleting paragraphs (d) and (e)).

A ballot was taken with the following result:
In favour 172.

Against 167.

(A further discussion took place on the following Tuesday afternoon when the ad hoc committee presented their decisions.) p. 508.

Recommendation IX

PROP. 1	(13: 209)	Rejected.
PROP. 2	(11: 196)	Rejected.
PROP. 3	(30: 186)	Rejected.

New Recommendation IXa

PROP.	(7: 104)	Rejected.
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Article 23

PROP. 1	(28: 152)	Rejected
PROP. 2	(20: 190)	Rejected.

Dr. A. C. SMITH said that his proposal 2 under Art. 23 (page 50) was made in case his proposal 6 under Art. 21 (page 38) should be accepted. This was accepted as amended by Prof. LANJOUW. This made para. 4 of the present Article redundant and it should accordingly be deleted. This deletion would not mean elimination of an appendix of conserved family names which he favoured. Such an appendix could then be authorised by the revised Art. 21. The wording of the footnote on the present Art. 21 Note 1 should be changed merely by substitution of

lists for list, especially if taxa of a higher rank than families are included.

Provisions for conserving names of whatever category seem to belong to Section 3, not Section 4, and he hoped the Rapporteur would reconsider his comment pertaining to his proposal 2.

Prof. MERRILL asked if a re-vote was wanted by Dr. SMITH.

Dr. SMITH said he would like to have Prof. LANJOUW's reasons for saying that acceptance of Prop. 2 was not recommended.

Prof. LANJOUW said he had thought that Dr. SMITH did not want to conserve names of families; he had misinterpreted Dr. SMITH's proposal.

Dr. RAMSBOTTOM thought such paragraphs as this should be given once and for all and that in their most appropriate position. They should not be repeated, as this often leads to confusion. They should merely be referred to when necessary.

Prof. LANJOUW moved that Art. 23 Prop. 2 of Dr. SMITH be accepted.

Prof. MERRILL put this to the vote by show of cards. It was *carried* unanimously.

PROP. 3 (27: 155) Rejected.

PROP. 4 (19: 185) Rejected.

Although rejected, it was agreed to refer these proposals to the Editorial Committee to take note of the examples.

PROP. 5 (180: 55) *Accepted*.

Prof. LANJOUW said that we were faced with the question as to whether we should allow alternative endings for certain family names. He states that he is in favour of no exceptions.

PROP. 6 (111: 101)

Dr. BOIVIN moved to vote again on Prop. 3.

Dr. FOSBERG said that the Utrecht symposium recommended the acceptance of Prop. 6. Prop. 6 has no relation to Prop. 5.

Dr. BOIVIN thought a vote might be taken as to whether or not we should have exceptions.

Dr. CAMP seconded this.

Prof. ST. JOHN said that the present Art. 23 adopted in Amsterdam validated the use of two alternative names for certain specified family names. He thought it was very confusing and unfortunate to have two names valid for a single family. He urged that we should come to a decision which would make only one of the two names valid. Since *Palmae*, *Leguminosae*, *Gramineae* have been in very wide use for centuries, he would regret having to abandon them, and urged that their special status should be continued.

Dr. SPRAGUE recalled that the provision allowing the use of alternative names in *-aceae* was accepted at Cambridge in 1931 on a motion of BAENHART, and that he himself had supported it in the spirit of cordial collaboration which had prevailed at that Congress. The late Dr. BRIQUET, as Rapporteur général, had pointed out, however, that the acceptance of alternative names was contrary to the principle that each group could bear only one valid name (Rep. Fifth International Botanical Congress, 1930, pp. 623, 4). The question now was: Shall we have these alternative names?

Prof. MERRILL put a motion for the acceptance of alternative names to the vote by secret ballot.

SESSION 6

July 10th, 2—5.55 p. m.

Chairman: T. A. SPRAGUE

The result of the ballot on the acceptance of alternative names for certain families was declared as follows:

In favour 175.

Against 176.

Dr. SPRAGUE thought that a majority of one

vote was too small to justify change in the existing Rules, and suggested that the result of the voting should be treated as a tie. A motion to this effect was proposed by Dr. BOIVIN and seconded by Dr. BLAKE.

A vote by show of cards was taken and the motion was *carried* by a very large majority only five voting against it.

Dr. CAMP noted that Prop. 3 of Art. 23 was similar (actually equal) to Prop. 2, Appendix II, p. 219. He moved that *the fixation of alternative family names be referred to the Special Committee concerned with the conservation of family names*.

This was put to the vote and *carried*.

Mr. GILMOUR proposed that in order to gain time no speaker be allowed more than two minutes, and that no speaker be allowed to speak on the same proposal more than once without special permission from the Chair.

Mr. ATRY SHAW seconded the motion, which after a short discussion was *carried* by show of cards by a large majority.

Article 24

PROP. 1	(49: 123)	Rejected.
PROP. 2	(6: 181)	Rejected.
PROP. 3	(26: 171)	Rejected.
PROP. 4	(182: 41)	<i>Accepted.</i>
PROP. 5	(217: 7)	<i>Accepted.</i>

Prof. PAPENFUSS said that the tribal termination *-ae* is the one used for classes in *Algae* and an exception should perhaps be made in the case of *Algae*, unless it is correct to regard the termination *-phyceae* as correct for the classes of *Algae*.

Dr. SPRAGUE said this was a matter for consideration by the Algological Committee.

Article 25

PROP. 1	(4: 224)	Rejected.
PROP. 2	(23: 192)	Rejected.
PROP. 3	(143: 73)	

Dr. ROGERS proposed that this be referred to the Editorial Committee.

Dr. RICKETT seconded the proposal, which was agreed.

Recommendation X

Dr. SPRAGUE suggested the following wording "Botanists who are forming generic names should comply with the following Recommendations."

This was referred to the Editorial Committee.

PROP. 1 (119: 90)

PROP. 2 (170: 50)

It was agreed to refer these proposals also to the Editorial Committee.

PROP. 3 (20: 207) Rejected.

Article 26

PROP. 1 (46: 169) Rejected.

PROP. 2 (1: 196) Rejected.

PROP. 3 (153: 56) *Accepted.*

PROP. 4 (9: 199) Rejected.

PROP. 5 (65: 108)

Dr. HYLANDER said we should have all sub-generic names in the form of substantives in the singular number. Sections and lower supra-specific taxa should be designated either by substantives in the singular number or by adjectives in the plural.

Prof. BAEHNI proposed to retain only the last paragraph of Dr. HYLANDER's proposal "The same subdivisinal name . . . based on the same type, as proposed by Rapporteur.

Prof. HOCHREUTNER supported this, as also did Dr. BOIVIN.

Dr. DONK said the motion was to retain the last paragraph of the proposal. He said that quite a similar paragraph is found under Art. 30 (Syn. p. 70). The fact of the similarity between the two, already indicates that we are dealing with epithets rather than with names in Art. 26. At the Cambridge Congress the then Rapporteur général, (Briquet), considered "names" of subdivisions of genera as names (calling them associations), and not as is the case with specific names, as part of combinations. His arguments were very weak and

could hardly be more because we are indeed dealing here with epithets. One argument was not brought forward at the time, viz. that if he were correct Art. 61 would be applicable. This use of "names" here would also mean that a subdivision of a genus would be named without any mention of its genus.

Dr. SPRAGUE recalled that in 1929 the British Sub-Committee on Nomenclature (Brit. Prop. pp. 12, 38, 39) had proposed to treat the names of subdivisions of genera as binary combinations more or less analogous to the binary combinations used for species, and that they had regarded the second half of such combinations as "epithets" since they could not be repeated under the same generic name. He now thought that the late Dr. BRIQUET's term "association" was perhaps preferable to "combination," since the first and second terms were not directly combined, but were separated by the words subgenus, section, series, etc.

Mr. DANDY thought it was a very important point that subgeneric names should be considered as composed of *generic name* plus *subgeneric epithet*. As Dr. DONK had said, if subgeneric epithets were treated as names in themselves then they become subject to the homonym rule, so that the same subgeneric epithet could not legitimately be used under different genera.

Dr. SPRAGUE ruled that there should be two votes, the first on Prop. 5, excluding the last paragraph, and the second on the last paragraph with its example.

Votes were taken by show of cards with the following results:

PROP. 5 *first part*.

Rejected by a large majority.

PROP. 5 *last paragraph with its example*.

Accepted by a large majority.

New Article 26 bis

PROP. (153: 49)

It was decided to postpone any discussion on this proposal until Prof. LANJOUW who was absent should return to the meeting (see p. 497).

Recommendation XI

PROP. 1	(60: 122)	Rejected.
PROP. 2	(46: 125)	Rejected.
PROP. 3	(108: 62)	Accepted.
PROP. 4	(5: 178)	Rejected.

Recommendation XII

PROP. 1	(22: 189)	Rejected.
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Article 27

PROP. 1	(4: 226)	Rejected.
PROP. 2	(6: 219)	Rejected.
PROP. 3	(34: 200)	Rejected.
PROP. 4	(182: 51)	Accepted.

Dr. DONK said that the proposal speaks of specific epithets under the word "Anonyms" as being *illegitimate* and calls them moreover *binary combinations*.

A few days ago he drew attention to the use of "illegitimate" in Prop. 4 under Art. 16 (this Synopsis pp. 17 and 18), where illegitimate combinations with a generic name have been accepted as fit for purposes of priority. He did not object to that, but at that time wanted to be assured that "illegitimate" in the accepted part of that proposal should not cover also "not validly published", because he was not at all certain that the difference between the two terms, (illegitimate and not validly published) was evident to a part of this meeting.

In the two cases under discussion we deal with combinations with a word and combinations with a name respectively. The situation in the present case is indeed different, but the use of "illegitimate" here should be objected to and this term be replaced by "not validly published."

Dr. BOIVIN said he wished to raise the same point.

Dr. SPRAGUE said that Dr. DONK and Dr. BOIVIN should submit any proposed emendations of the text of Art. 27, Prop. 4, to the Editorial Committee.

Dr. BLAKE said that the matter concerned

only North American plants, and the treatment of WALTER's names under *Anonymos* as illegitimate caused no inconvenience.

Dr. SPRAGUE said that only two of WALTER's epithets were lost through treating these combinations as illegitimate (see LANJOUW, Bot. Nomencl. and Tax. 1950, p. 21). The combinations were validly published, being effectively published and accompanied by descriptions (Art. 37), but were illegitimate since, contrary to Art. 27, they were not combinations consisting of a generic name and a specific epithet.

PROP. 5	(1: 221)	Rejected.
PROP. 6	(23: 205)	Rejected
PROP. 7	(203: 25)	Accepted.

Article 28

PROP. 1	(7: 205)	Rejected.
PROP. 2	(40: 158)	Rejected.
PROP. 3	(67: 129)	

Dr. DE WIT suggested that "subspecific" should be replaced in the proposal by "intra-specific" or "subordinate."

Dr. BOVIN moved that the principle be accepted and the text left to the Editorial Committee. This was agreed.

Dr. FOSBERG pointed out that this was essentially the same as Prop. 5 which had been accepted in the preliminary voting.

PROP. 4	(11: 190)	Rejected.
PROP. 5	(180: 53)	Accepted.

To be sent to the Editorial Committee.

PROP. 6	(9: 202)	Rejected.
PROP. 7	(6: 203)	Rejected.
PROP. 8	(26: 147)	Rejected.
PROP. 9	(2: 200)	Rejected.

Recommendation XIV

PROP. 1	(14: 231)	Rejected.
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Recommendation XIV bis

PROP.	(0: 220)	Rejected.
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Recommendation XV

PROP. 1	(204: 36)	Accepted.
PROP. 2	(5: 192)	Rejected.

New Article 28 bis

PROP.	(150: 76)	
PROP.	(50: 160)	

Discussion on these proposals was postponed until Prof. LANJOUW's return (see p. 497).

New Article 28 ter

PROP.	(1: 221)	Rejected.
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Article 29

PROP. 1	(9: 228)	Rejected.
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Article 30

PROP. 1	(25: 167)	Rejected.
PROP. 2	(2: 215)	Rejected.
PROP. 3	(28: 191)	Rejected.

New Article 30 bis

PROP.	(6: 215)	Rejected.
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New Article 30 ter

PROP.	(29: 204)	Rejected.
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Recommendation XVIII

PROP. 1	(137: 86)	
PROP. 2	(132: 78)	
PROP. 3	(1: 192)	Rejected.
PROP. 4	(13: 178)	Rejected.
PROP. 5	(10: 176)	Rejected.
PROP. 6	(126: 81)	
PROP. 7	(6: 181)	Rejected.
PROP. 8	(121: 90)	
PROP. 9	(15: 182)	Rejected.

Proposals 1, 2, 6 and 8, that Rec. XVIII be deleted, had not received the two-thirds major-

ity in the preliminary voting required for automatic acceptance. A *motion for the deletion of Rec. XVIII* was therefore put to the vote by show of cards, and *carried* by a very large majority.

Recommendation XIX

PROP. 1 (123: 91)

Mr. AIRY SHAW proposed that Rec. XIX Prop. 1 be accepted, and this was seconded by Dr. CAMP.

Dr. SPRAGUE said that although it might be practically impossible to follow Rec. XIX as to epithets which had been used previously for *subdivisions* of other species in the same genus, it was—except in very large genera such as *Hieracium* and *Rubus*—easy to do so in the case of epithets which had been used previously for *species* in the same genus, since these were listed in the Index Kewensis and its Supplements. He accordingly suggested the acceptance of the following revised wording of Rec. XIX:

“Botanists proposing new epithets for subdivisions of species should avoid such as have been used previously for species in the same genus.”

Dr. FOSBERG said that as there was nothing mandatory about the Recommendation he did not see why it should be deleted. The *proposed new wording was put to the vote* by show of cards and *carried* unanimously.

New Recommendation XIX bis

PROP. (6: 225) Rejected.

Section 4 § 6. Names of hybrids and half-breeds

This has already been dealt with (see p. 482–485).

Section 5. Conditions of effective publication

PROP. 1 (5: 190) Rejected.

PROP. 2 (210: 38) Accepted.

Article 36

Dr. SPRAGUE made some introductory remarks on the conditions of effective publication. He drew attention to the publication of “Candollea.” It appears in parts and is distributed to Institutions etc. as a whole. He said that Prof. BAEHNI had told him that the separates from “Candollea” were placed on sale, though few were actually sold. He had suggested the addition of the words “Provided that the separates themselves are placed on sale” in order to prevent priority being obtained for names *before* they were accessible to the general public or to Botanical Institutions.

Prof. BAEHNI confirmed the statement regarding the issue of the separates from “Candollea.”

PROP. 1 (160: 64) Accepted.

Dr. SPRAGUE suggested that the words “up to and including” might be clearer than “through.”

PROP. 2 (1: 223) Rejected.

PROP. 3 (17: 195) Rejected.

PROP. 4 (128: 108)

Dr. FOSBERG said that catalogues were ephemeral publications, not usually filed in libraries, and were hard to locate.

Dr. CAMP thought that many good and accepted names occurred in old catalogues, (seedsmen's and nurserymen's), and that in order to avoid further chaos we must accept them. He thought it would be satisfactory to have a limiting date, after which publication in such catalogues would be non-effective.

Prof. LAWRENCE thought that, contrary to Dr. FOSBERG's views just expressed, there were good collections of catalogues in the United States, at least four in Britain, one in the Netherlands, one in Geneva and others elsewhere. Many well-established names would be upset if this provision were made retroactive.

Miss EASTWOOD emphasized the disadvantages of not taking up these old names found in catalogues; she cited some of PURDY's names

from his catalogue, where she said the first description of the plants also occurred.

Dr. SPRAGUE remarked that these were very telling examples.

Prof. LAWRENCE thought that the date 1935 might be fixed as a starting point for the proposal.

Prof. BAEHNI also thought a starting point was necessary, if this were agreed he would support the proposal.

Dr. HYLANDER suggested Jan. 1st 1952 as the starting point.

Prof. HOCHREUTINER demande pourquoi on met les tirés à part dans une catégorie différente de celle des livres? Leur date, en effet, est acceptée, à moins de preuve du contraire, pourquoi ne pas ajouter cela pour la date des livres? C'est jeter la suspicion sur les tirages à part.

Prof. MATTFELD: Eine Zeitschrift, die alle Diagnosen sammelt, macht diese Vorschriften überflüssig.

Prof. HOCHREUTINER said that there were to be found very good published names in old catalogues such as were in DE CANDOLLE's Library. He said that he thought we could only rule for the future.

Prof. ROUSSEAU said that personally he sympathised with Dr. FOSBERG's proposal, and this would confirm a name he had already proposed, but he drew attention to the fact that all the names proposed by MARSHALL in his "Arbustum Americanum" would have to be abandoned. Consequently we should have to choose new names for many North American plants.

Dr. SPRAGUE summed up and proposed that, in view of such works as PURDY's Catalogue mentioned by Miss EASTWOOD and MARSHALL's Arbustum Americanum mentioned by Dr. ROUSSEAU, the provision should not be retroactive. Should the starting date be Prof. LAWRENCE's date 1935 or Dr. HYLANDER's 1952?

Prof. LAWRENCE agreed to Jan. 1st 1952.

Mr. DANDY said that, while he agreed with the proposition in principle, he would like to ask what is the definition of a newspaper. He

believed that several journals accepted by botanists as mediums of publication were registered as newspapers. What was to be done about this?

Dr. SPRAGUE referred to Art. 36, Prop. 9 of Dr. HYLANDER paragraph 4: "*From Jan. 1st, 1952, the publication of a new name, even if accompanied by a Latin diagnosis, in tradesmen's catalogues or in newspapers is not considered as effective publication.*" This he said was similar to Dr. FOSBERG's proposal with the date added.

It was decided to vote on this with the result that it was carried by a very large majority.

The vote means the following addition: From Jan. 1st 1952, the publication of a new name, even if accompanied by a Latin diagnosis, in tradesmen's catalogues or in newspapers is not considered as effective publication (para. 4, Prop. 9).

PROP. 5 (22: 191) Withdrawn.

This was withdrawn by Dr. SPRAGUE, who explained that it had been impossible to reach agreement on the proposed list of representative Botanical Institutions. See LANJOUW, Bot. Nomencl. and Tax. 1950, pp. 32, 33.

PROP. 6 (28: 160) Rejected.

Dr. DE WIT said he had employed the words "a reasonable number of copies" because according to the present Rules, TEYS. and BINN. Catalogue of 1854 known only in two copies (of which one was recently lost) contains valid names which if followed up would involve more or less 40 name changes, even of one or two American plants. He thought two copies unreasonable and that the point ought to be clarified. He also mentioned certain difficulties that had arisen during the war years over the distribution of certain periodicals, but it was decided that it was better to treat such cases on their own merits rather than to attempt to deal with them by a special provision in the Rules.

PROP. 7 (2: 204) Rejected.

PROP. 8 (26: 193) Rejected.

Mr STEVENSON, the joint author of Prop. 8, asked whether if this proposition were rejected,

it would be possible to have the subject matter used as an example.

Dr. A. C. SMITH supported Prop. 8. Microfilm publication he considered was not desirable. The proposal was an excellent one, not covered elsewhere in the Rules.

Dr. ROGERS thought that as the matter is not covered elsewhere in the Rules, the italicised parts of Prop. 8 might be adopted.

Dr. BLAKE thought it would be easy to make one microfilm copy and thus meet the requirement for the "existence of the material."

Dr. FOSBERG considered that such a case is not merely hypothetical. It actually is the practice to make at least one microfilm, this practice will become more frequent in the future if permitted.

Dr. ROGERS agreed with Dr. FOSBERG and withdraw his suggestion.

Mr. STEARN spoke against considering the making of a microfilm from a manuscript deposited in a library, as effective publication. It is always possible for an alteration to be made in a manuscript, even in one deposited in a library, between the making of one microfilm and another.

Dr. SMITH wanted to vote on Prop. 8 as worded in the Synopsis.

Dr. PATRICK said that in the United States a great deal of pressure is being made to publish doctoral theses dealing with taxonomy by microfilm etc.

Therefore we should either affirm or reject methods similar to microfilm and microprinting.

Dr. RICKETT thought that if it is the sense of the meeting that microfilm is not an acceptable means of publication, the proposal should make this more clear and he suggested to substitute for the italicised words "or the issue of microfilms made from manuscripts."

Dr. BLAKE said that microprinting was involved. He wondered if the matter could be referred to a Committee.

Dr. HYLANDER thought a definition of "printed matter" was needed.

Prof. HOCHREUTINER signale que les microfilms constituent seulement une possibilité de

publication et non pas une publication elle-même. C'est seulement si la production d'un micro-film atteint 200 ou 300 exemplaires qu'on pourrait appeler cela une publication, et encore, cela est contestable.

Prof. ROLLINS said that new methods of printing are in course of development, and we should not stultify their possible advantages to botany by ruling in advance against them. Therefore the wording of any limitation should be carefully drawn.

It was then suggested that Prof. WEHMEYER and Dr. STEVENSON should consider rewording their proposal, and bring it up later on.

PROP. 9 (28: 177) Rejected.

As has been stated above, para. 4 of this proposal has been accepted.

PROP. 10 (5: 209) Rejected.

PROP. 11 (203: 25)

Dr. BOIVIN said that this proposal means that the footnote to Art. 36 should be deleted.

Dr. SPRAGUE said that would automatically be done.

Prof. LANJOUW said he would like to point out that there might be added to this Article that all publication of new names should be sent to the Bureau of Taxonomy which he thought would be formed.

Dr. BLAKE asked if Prop. 11 were accepted would it rule out Wallich's catalogue?

Dr. SPRAGUE agreed, but doubted whether any accepted names would be lost thereby.

Dr. CAMP said many machines were called "printing machines."

Prof. LANJOUW said microprinting was printed matter.

Mr. ROSS said that Prop. 11 covers microcards, but not manuscript deposited with microfilm reproduction permitted.

Dr. HYLANDER moved that Prop. 11 be accepted.

Dr. RICKETT said that printed matter is very hard to define in such a way as to exclude microfilm. Prop. 8 does not accomplish this. "Printing" is the reproduction of identical co-

pies from a matrix—whether film or paper is used it would not be practical to say.

Dr. SPRAGUE said that the Section must decide whether they wished to vote on Prop. 11 with the addition of the sentence from Prop. 8.

Mr. STEARN proposed the addition of the words "unless there is evidence to the contrary" to the third paragraph of Art. 36.

Dr. FOSBERG wished to accept Prop. 11 as it stands and Prop. 8 as amended by Dr. RICKETT replacing the italicised words by "or the issue of microfilm made from manuscripts" and to add to para. 3 "unless there is evidence to the contrary."

Dr. FOSBERG then read the whole text of the revised Article.

Art. 36 as amended. Publication is effected under these Rules, by distribution, by sale, by exchange, or otherwise of printed matter. No other kind of publication is accepted as effective: communication of new names at a public meeting, or the placing of names in collections or gardens open to the public, or the issue of microfilm made from manuscripts does not constitute effective publication. Up to and including Dec. 31st 1951 publication by indelible autograph is accepted.

Offer for sale of material that does not exist does not constitute effective publication.

When separates from periodicals or other works placed on sale are issued in advance, the date on the separate is accepted as the date of effective publication unless there is evidence to the contrary.

On and from Jan. 1st 1952 the publication of a new name, even if accompanied by a Latin diagnosis, in tradesmen's catalogues or in newspapers is not considered as effective publication.

Note. For purposes of this Article handwritten material, even though reproduced by some process such as lithography, offset, metallic etching or microfilm is still considered autographic.

Dr. ROGERS gave an example of *Selaginella* species published by HIERONYMUS in Hedw. 51: 241-272. 1912. They were validly published on Oct. 15th, 1911, even though the date

does not appear on the separate, since the volume in which the paper appeared states (p. (II)) that the separate appeared on that date.

This was referred to the Editorial Committee as an oblique example of the application of the phrase "unless there is evidence to the contrary" in Art. 36 as amended.

Dr. FOSBERG said that Mr. STEARN could also give an example.

A motion for the acceptance of the new wording of Art. 36 was then put to the vote and was carried unanimously.

New Recommendation XX bis

PROP. (139: 88)

New Recommendation XX ter

PROP. (164: 64)

Prof. PAPENFUSS said he would like to ask that the publication of species in exsiccatae be outlawed along with those under discussion. After a very short discussion it was decided to vote on the acceptance of the first part of XX bis down to "general botanical public" and to add to it the last sentence of XX ter "or in those produced by such methods that their permanence is unlikely."

Dr. SPRAGUE called for a vote by show of cards, and the motion was carried unanimously.

New Recommendation XX quater

PROP. (106: 93)

Prof. HOLTUM called attention to the fact that he had proposed a change in Art. 37 which would have the same effect as Rec. XX quater with the force of a Rule.

Prof. LANJOUW did not consider this was a very important recommendation but there was nothing against it.

Dr. BOIVIN thought the editors should delete the first three words "from 1950 onwards."

Dr. DONK thought it might be preferable to deal with this new Recommendation in connection with Art. 37, 42 and 44, where it is pro-

posed to delete the words "under another name."

Under the present Rules the proposition under discussion conflicts with the Articles mentioned, which prescribe that the reference should be to a description under another name. Leaving out of account the word "another" for the moment, "name" means in these Articles "a validly published name," see Art. 19. Because pre-Linnean names are not validly published, a new name cannot be validly published by a reference to a pre-Linnean description. Dr. SPRAGUE explained that under the Rules, pre-Linnean literature, including both descriptions and names, was effectively published, if it complied with Art. 36. Publication of descriptions and names could accordingly be *effective* from the date of the invention of printing, whereas *valid publication of names* did not start until 1753 (or later in certain cases). Those who held that pre-Linnean descriptions were not effectively published were confusing taxonomy with nomenclature: botanical *taxonomy* started long before 1753, though recognised botanical *nomenclature* began at that date. Pre-Linnean descriptions and figures had often to be taken into account in order to determine the correct application of Linnean names. From the time of Linnaeus onwards, the publication of numerous names of taxa had been validated by references to effectively published pre-Linnean descriptions. *Pyrolirion albicans* Herb. (now known as *Cooperia albicans*) was a case in point, being based solely on a description and figure published by FEUILLEÉ.

Under the present wording of Art. 42 and 44, the publication of a name of a genus or species was validated by reference to a pre-Linnean description, if the pre-Linnean author had used a *different* name for the taxon, but not if he had used the *same* name. The new wording was designed to remove this absurd anomaly.

It would be highly undesirable to introduce into the Rules a new and retroactive provision, outlawing many names published according to accepted practice during the past two centuries. He thought however that this method of valida-

tion might perhaps be prohibited in the *future*, say from Jan. 1st 1952.

Mr. DANDY preferred that this matter be treated as a Recommendation, and that names based on pre-Linnean literature should not be definitely prohibited. There are cases in which the sum total of our knowledge of a plant is confined to pre-Linnean literature, and such plants should be named.

Dr. HYLANDER recommended the *acceptance of the first sentence of Rec. XX quater*, and deletion of the second sentence.

Dr. SPRAGUE put this to the vote by show of cards and it was *carried* with a very large majority.

On a question as to the precise wording of the Recommendation, Prof. MERRILL said the wording would be considered by the Editorial Committee.

New Recommendation XX quinques

PROP. (19:185) Rejected.

New Article 36 bis

PROP. (89:98)

Dr. SPRAGUE asked Dr. DE WIT if he wished to speak as author of the proposal.

Dr. DE WIT said he thought it was necessary to establish the day of publication whenever possible. The necessity for this had already been clearly felt in the case of the various starting points. This proposal is a first step towards a clearer understanding of the moment of publication, which is of utmost importance in cases of close priority.

Prof. LANJOUW thought para. 3 could be deleted.

Prof. BAEHNI thought para. 4 could be deleted.

Dr. RAMSBOTTOM suggested the word "volume" in place of "work."

Dr. CAMP thought unfortunate as was the situation the Rules should not include such things as reminders of events as found in the examples given under the proposals.

Prof. HOCHREUTINER demande de préciser ce qu'on entend par "work" en anglais? Faut-il le traduire par "ouvrage" ou "livre?" Si c'est un livre, ce peut être un périodique, mais nous y sommes opposés et nous nous basons sur ce qui a été décidé à propos de "Candollea."

Les 2 premiers paragraphes de cet article sont acceptés.

Dr. DE WIT considered the objections were entirely reasonable and he withdrew all (including examples), except paragraphs one and two.

Dr. SPRAGUE moved that we adopt paragraphs 1 and 2 of Art. 36 bis and called for a vote by show of cards.

The motion was carried by a large majority.

New Article 36 ter

PROP. (91: 97)

Prof. LANJOUW drew attention to his comments in the Synopsis on this article of Prof. HUMBERT. It was agreed this proposal could not be made retroactive.

Dr. HYLANDER drew attention to his Prop. 9 of Art. 36, last paragraph and note.

Some of the members preferred Prof. HUMBERT's wording and some Dr. HYLANDER's.

Dr. RAMSBOTTOM proposed the wording of Prof. HUMBERT and the example of Dr. HYLANDER, if approved by the Editorial Committee. He also said that a question arises about the status of booklets issued with exsiccatae which give the descriptions of new species and whether they are placed on sale or not.

Dr. HYLANDER withdrew his proposal on the understanding that the "note" be referred to the Editorial Committee.

Dr. SPRAGUE called for a vote on Art. 36 ter as it stands. The Article was carried by a very large majority.

Those Articles postponed during the earlier part of the session in order to await Prof. LANJOUW's return were next considered.

Article 26 bis

PROP. (153: 49)

Article 28 bis

PROP. (150: 76)

PROP. 1 (58: 160)

On a proposal by Prof. LANJOUW it was decided to consider Art. 28 bis first. He pointed out that his new Art. 28 bis and Dr. GLEASON's Prop. 1 differed only very slightly. He said that his version was accepted by the Utrecht Conference, and Dr. GLEASON's was accepted with a slight majority by the American botanists.

Dr. RICKETT said the essential difference between the two versions is in the use of the words "taxon" and "infraspecific." He said that the change was acceptable to Dr. GLEASON.

Mr. ROSS pointed out that the second paragraph of Dr. GLEASON's proposal covers a point not covered by Prof. LANJOUW. This is needed also and should be incorporated, edited as necessary.

Prof. LANJOUW agreed.

Dr. BOIVIN moved that the principle embodied in the following proposals be accepted and that the text be left to the Editorial Committee:

Art. 28 Prop. 3 (Gleason).

Art. 28 Prop. 7 (Botanistes Belges).

New Art. 28 bis (Lanjouw).

Art. 28 bis Prop. 1 (Gleason).

Art. 30 bis (Boivin).

Rec. XXXV Prop. 3 (Boivin).

Dr. FOSBERG thought Art. 28, Prop. 7 rather different.

Dr. SPRAGUE said the Editorial Committee would certainly take all into account.

Prof. HOCHREUTINER trouve que la proposition LANJOUW est un progrès très important et il la recommande à l'assemblée.

Prof. ROBYNS preferred the text of Prof. LANJOUW.

Dr. SPRAGUE called for a vote on the new Art. 28 bis and the other proposals mentioned by Dr. BOIVIN to be taken into consideration by the Editorial Committee.

The vote was carried by a very large majority.

New Article 26 bis

PROP. (153: 49)

Prof. BAEHNI suggested the deletion of the words "if no earlier legitimate name is available."

Prof. LANJOUW agreed to this amendment.

Mr. STEARN pointed out that the use at one and the same time of the same name for two groups of different circumscription, for the genus and for one of its subdivisions, was likely to lead to lack of precision or else awkwardness of expression when discussing such matters as geographical distribution, cytology, phylogeny, etc., which concern both; it would be necessary always to state whether the genus or the subdivision was meant instead of this being clear from the names alone. Moreover, in some genera there is uncertainty as to which species should be taken as the type, and this would be re-

flected in uncertainty and liability to change in subdivisional names. The genus *Anemone* in which *A. nemorosa* has been selected as the type species by some, but for which on historical grounds a monographer would prefer *A. coronaria* is an example: there exist good sectional names already and this new rule is accordingly undesirable.

Prof. LANJOUW said that if you are in such an awkward position that you cannot typify a particular generic name you cannot apply this rule.

Dr. HYLANDER suggested that the term "subgenus" might be used instead of "subdivision."

Prof. LANJOUW agreed.

Prof. LAM suggested that the Editorial Committee should add an example.

Dr. SPRAGUE: *Then put to the vote the New Art. 26 bis as amended.*

This was carried by a large majority.

SESSION 7

July 11th, 9.30 a. m. — 12.30 p. m.

Chairman: E. D. MERRILL

Section 6. Conditions and dates of valid publication of names

PROP. 1 (26: 69)

PROP. 2 (28: 62)

Prof. MERRILL moved that the Editorial Committee be asked to consider both these propositions. This was agreed to.

Article 37

PROP. 1 (74: 101)

Prof. LANJOUW explained that the first part of this proposal belongs under Art. 37 bis.

Dr. ROGERS pointed out that a decision on paragraph 2 had been taken on the previous day.

Prof. LANJOUW agreed that only the first part remained.

The proposal was also dealt with under Prop. 3 of Art. 37 bis by Dr. FOSBERG.

Prof. MERRILL moved that it be deferred till Prop. 3 of Art. 37 bis be dealt with.

This was agreed.

PROP. 2 (2: 222) Rejected.

PROP. 3 (6: 190) Rejected.

PROP. 4 (195: 39)

Dr. SPRAGUE said that the example under Prop. 4 explained the reason for his proposal. In the case of *Cymbopogon martini* the publication of the name was validated by the addition of the number "309" which was the run-

ning number in STEUDEL's Syn. Pl. Glum. Thus it was an indirect or implicit reference.

Prof. HOLTUM suggested that the term "implicit reference" needs to be clearly defined, as otherwise it would lend itself to abuse.

Prof. MERRILL moved the acceptance of Prop. 4 (SPRAGUE).

By show of cards this was *carried* almost unanimously.

PROP. 5 (8: 190) Rejected.

PROP. 6 (106: 82)

This was postponed until Art. 37 bis Prop. 3 was considered.

PROP. 7 (207: 20)

Dr. BOIVIN moved the following change in Prop. 7 instead of "its author, date, and place of publication" read "proper bibliographic reference."

Dr. SPRAGUE pointed out that the Section had already approved Prop. 4 concerning "indirect reference."

Dr. HYLANDER thought Prop. 4 (SPRAGUE) and Prop. 7 (FOSBERG) could be combined.

Prof. BAEHNI said he did not think the French language had a word for basonym.

Dr. DE WIT thought that Prop. 4 and 7 did not really contradict each other. If the term basonym were used, he thought it should be spelt basynym.

Dr. SPRAGUE gave the derivation of *basonym* from *basis* (βάσις) and *onyma* (ὄνυμα) and said that in such combinations formed from two Greek words the second of which began with a vowel, that vowel was retained, e.g. *antonym* (from *anti* and *onyma*), *metonymy* (from *meta* and *onyma*).

Dr. DONK suggested that this proposal should rather be taken up in connection with Art. 42 Prop. 2. He asked if basonym is left out, whether that would imply that a reference to a misapplied name could make a new name validly published.

Prof. HOCHREUTINER suggested that the word basonym should be defined.¹

¹ "qu'une note au bas de la page devra expliquer le mot 'Basonymes' s'il figure dans le texte."

Dr. BOIVIN suggested that should be referred to the Editorial Committee.

This was agreed.

Mr. STEARN proposed to add as a note the following:

"An error of citation resulting from a misprint or the author's ignorance of the precise date of publication does not, however, invalidate the transfer or new name."

Prof. MERRILL wished to call for a vote on the motion.

Dr. HYLANDER asked if his proposals 45 bis and 45 ter could be taken into consideration.

Prof. LANJOUW gave the preliminary voting on these.

Art. 45 bis (19: 192)

Art. 45 ter (23: 194)

Prof. MERRILL said that although automatically rejected the Editorial Committee might, if they so desired, consider them.

Mr. STEARN asked about his note.

Prof. MERRILL suggested that that too should go to the Editorial Committee.

Prof. LANJOUW said they might also insert the word "however" after "new Combinations" in Art. 37 Prop. 7.

Prof. MERRILL then moved that a *vote be taken on Art. 37, Prop. 7 as amended*, and that the final draft should be left to the Editorial Committee, who would take note of Dr. BOIVIN's amendment and Mr. STEARN's note.

This was *carried* almost unanimously.

PROP. 8 (225: 4)

Prof. MERRILL put this to the vote and it was unanimously *accepted*.

PROP. 9 (10: 181) Rejected.

Article 37 bis

PROP. 1 (21: 202) Rejected.

PROP. 2 (23: 189) Rejected.

PROP. 3 (185: 44)

Prof. LANJOUW pointed out that there had been some complaint concerning the text of this Article. It had been drawn up by Dr. SPRAGUE and himself, and they had felt that

the present text was clearer than that proposed at Amsterdam. He felt, however, in the circumstances that the Section should vote on this as a new proposal.

Dr. SPRAGUE read the original text from the Amsterdam Report, p. 365. The new wording concerned mainly the substitution of the word "eventual" by "future," as the word "eventuale" was used in a different sense on the Continent and it had been decided at Amsterdam that the words "seu eventuale" should be omitted.

Dr. DONK asked whether the present Art. 37 bis would not be improved if in the first line "but" is replaced by "or."

Prof. MERRILL and Dr. SPRAGUE saw no objection to that.

Dr. BOIVIN moved that Art. 37 bis Prop. 3 be accepted, and that the present text and examples of 37 bis and Art. 37 Prop. 1 and 6 be referred to the Editors for consideration.

Prof. ROUSSEAU proposed to delete the note under 37 bis Prop. 3. He considered it was not advisable to retain it.

Prof. ST JOHN said that this proposal would validate the use of alternative names in the instance that the name was proposed for immediate use. He submitted that the distinction between names for immediate use and those for future use is one that is impossible to apply, since each subsequent use of a name is really a use in the future. Hence the proposition 3 would be impossible to apply with certainty.

Dr. HYLANDER pointed out the "note" under Art. 37 bis Prop. 3 was not the same as the "note" in the Report of the Utrecht Conference which was "This article does not apply to alternative names such as *Andropogon bequaerti* De Wild., which was proposed by DE WILDEMAN (Bull. Jard. Bot. Brux. vi p. 8, 1919) as an alternative name for immediate use by those who accepted the wider circumscription of the genus *Andropogon* previously in use."

Prof. ROBYNS expressed his agreement with this.

Dr. RICKETT said the attempt to distinguish "alternative" and provisional names is productive of trouble, and nothing is to be gained

by attempting to save "alternative" names. The note should be omitted, and the article reworded to exclude or invalidate all provisional and alternative names. The Prop. 6 of Art. 37 of Prof. ST JOHN para. 3 should be added as a note.

Prof. ROBYNS outlined the discussion that took place at Amsterdam concerning provisional and alternative names.

Mrs. SPRAGUE said that before 1935 it was customary to insert "*nom. provis.*" or "*nom. alternativ.*" in the Supplements of the Index Kewensis when required, but after 1935 it was considered wiser not to do this, as often it was very difficult to decide whether a name was provisional or alternative.

Dr. ROGERS thought the rule adopted at Amsterdam had proved sufficiently satisfactory for fourteen years. No difficulty had yet been reported. The text then adopted should be retained.

Dr. FOSBERG said he had never been able to understand Art. 37 bis. He thought Prop. 3 seemed much the clearest wording and would be very satisfactory with the addition of a provision disposing of alternative names.

Dr. MARTIN said that Dr. MURRILL had described hundreds of species assigning them to genera recognised by himself and those who follow him, and also assigning names for the same species if referred to another genus in use by other mycologists. These are therefore, alternative names, and under the interpretation suggested, neither would be validly published.

Dr. DONK said the example of MURRILL's names mentioned by Dr. MARTIN covered several hundreds of specific combinations.

Prof. MERRILL remarked another trouble for the Mycologists!

Dr. BLAKE stated that the precise meaning of the term "alternative name" was not clear to him. If an author describes a new species *Cymbopogon bequaerti* and give the alternative name *Andropogon bequaerti*, then *Cymbopogon bequaerti* is in a sense also an alternative name, because only one of these names can be used at a time. He judged from comments from the

audience that the primary name used by the author would not be regarded as an "alternative name."

Prof. HOCHREUTNER propose de supprimer la distinction des noms alternatifs et de les considérer comme valables, les deux alternatifs étant admis comme valablement publiés.

Prof. BAEHNI estime nécessaire de dire qu'un nom provisoire, donné à cause de l'ignorance de l'auteur du rang exact du groupe, est néanmoins valablement publié.

Dr. FOSBERG proposed that the note from Art. 37 bis Prop. 3 should be deleted and that there should be a vote on the proposal only.

Dr. BOIVIN seconded this—replacing "but" by "or."

He suggested that Dr. RICKETT's proposal should be considered next.

Prof. MERRILL put Art. 37 bis Prop. 3 as thus amended to the vote by show of cards.

It was carried almost unanimously.

Prof. LANJOUW then asked Dr. RICKETT to give the text of his proposal.

Dr. RICKETT "Alternative names shall be treated as not validly published."

Dr. SPRAGUE suggested the addition of "On and from Jan. 1st 1952."

Dr. BOIVIN proposed the following text "Before Jan. 1st, 1952 alternative names (nomina alternativa) are treated as validly published, but as illegitimate."

"Note: Both names are treated as illegitimate." He considered this as a re-affirmation of the Amsterdam proposal.

Dr. ROGERS said if this wording were accepted neither of the alternative names would be validly published, because both are alternative. The wording must be changed. One name of the two must not be regarded as alternative.

Dr. A. C. SMITH also thought the wording must be changed.

Prof. ST JOHN thought it should be pointed out when considering alternative names that there are two kinds. One author may publish two names, indicating that he accepts one name, but provides a second name for the authors who prefer the taxon in another position.

Another author may publish two names as full alternatives without giving any indication that he himself accepts one of them. It seems that these two methods of publishing alternative names are not equal.

Prof. MERRILL thought the first name might be chosen.

Dr. ROLLINS pointed out that the case where an author proposes alternative names without definitely accepting either was taken care of by the acceptance of the first portion of Prop. 3.

Prof. MERRILL then put to the vote the proposal of Dr. RICKETT with Dr. SPRAGUE's amendment "On and from Jan. 1st., 1952 alternative names shall be treated as not validly published."

The Editorial Committee to consider the best wording.

The proposal was carried by a very large majority.

Article 38

PROP. 1	(2:219)	Rejected.
PROP. 2	(2:227)	Rejected.
PROP. 3	(16:185)	Rejected.
PROP. 4	(23:115)	Rejected.
PROP. 5	(18:207)	Rejected.

The following discussion took place on Art. 38 Prop. 3.

Dr. HUSTEDT: Viele junge Naturwissenschaftler können kein Latein, weil die Kenntnis der lateinischen Sprache nicht mehr erforderlich ist. Viele algologische Floren bringen die Beschreibungen nur in einer neuen Sprache. In zusammenfassenden Floren mit Bestimmungstabellen, Beschreibungen und Abbildungen sind neue Einheiten als gültig anzuerkennen. Ein Appendix mit lateinischen Diagnosen würde die botanischen Werke verteuern. Tafelwerke können keine lateinischen Diagnosen geben. Wenn bei den Kollegen Toleranz erwartet wird, werden alle Regeln illusorisch. Daher soll man Gesetze erlassen, die auch ohne Toleranz innegehalten werden.

Ich empfehle daher die Vorschrift lateinischer

Diagnosen aufzuheben. Zu fordern ist eine Beschreibung in zwei Sprachen, von denen eine lateinisch, englisch, französisch oder deutsch sein soll.

Prof. W. VISCHER: Wichtige Werke, wie RABENHORST usw., bringen die Diagnosen nur in deutscher oder einer anderen modernen Sprache. Die Phycologen, und wahrscheinlich auch die Mykologen schlagen vor: Prop. 3 (LUND) zu Art. 38 in folgender Fassung anzunehmen, nachdem die Phycologen nochmals darüber beraten haben werden.

"The diagnoses of all algal taxa shall be given in two languages, one of which shall be Latin, French, German or English. The diagnosis of every alga new to science shall be accompanied by an adequate illustration and by the pertinent dimensions."

Prof. MATTFELD bemerkt dazu, dass diese neue Fassung des Prop. 3 die in einer modernen Sprache erschienenen Diagnosen nicht gültig macht, da ja jetzt zwei Sprachen vorgeschrieben werden; und da der Artikel rückwirkende Kraft hat, würde er alle bisherigen Algen-Diagnosen ungültig machen!

Prof. PAPENFUSS said that the Special Committee on Diatoms and Algae unanimously agreed that for these groups the requirement of a Latin diagnosis should be abandoned, and that Latin, French, German or English be substituted. He believed that it would be wise to delay action on this proposition until a more representative group of algologists have assembled to discuss this question.

Dr. BLAKE stated that the quality of most botanical Latin made it desirable to require two descriptions, one in Latin and one in the author's own language, in order that the author's meaning might be clearly indicated.

Prof. HEIM estime qu'il conviendrait de distinguer la diagnose, qui est une description concise et de valeur comparative, de la description que bien des botanistes, notamment les mycologues, ont tendance à détailler de plus en plus.

Si la diagnose devait toujours conserver cette définition concise, le maintien de la langue

latine se justifierait. Mais, dans l'état actuel de la connaissance insuffisante de cette langue, il paraît justifié d'ajouter les langues française et anglaise au latin, d'autant plus que ces deux langues vivantes sont les seules qui soient admises officiellement pour l'établissement de textes de juridiction internationale. Bien entendu, l'adjonction de la langue allemande pourrait être admise à condition qu'elle n'offre pas de nouvelle surenchère.

Dr. BOIVIN thought it was impossible to do Taxonomic Botany without a knowledge of Latin. He wished the present rule maintained. He thought it might perhaps be possible to put forward the date for compulsory Latin diagnoses in the Algae to 1953.

Dr. FOSBERG said that at present the rules require a Latin diagnosis. He regretted the tendency towards fragmentation in the Rules. Many people are not monographers, but are interested in many groups of plants. The Rules should be uniform for all groups. If we neglect Latin then national feelings may be aroused.

Dr. A. C. SMITH thought that Art. 38 should not be weakened by such additions as proposed by the Algologists.

Mr. ROSS said that as far as Algology is concerned Art. 38 is in contradiction to Art. 3. In work on the Diatoms he very rarely read anything written in Latin. Furthermore the Special Committees on Diatoms and Algae were unanimous in approving the principle of Art. 39 Prop. 3, with the addition of Latin as one of the alternatives.

Prof. SINGER thought that Art. 38 should be valid for all groups in Botany without exception. If Dr. HEIM's proposal should find a majority, I would move to include the Spanish language.

Dr. DONK said that if the Rules allow too many special provisions for valid publication of the different groups, it will become increasingly difficult to establish whether a name is a (generic) homonym or if it belongs to a group outside the field of the specialist who is trying to establish homonymy. He should prepare a card

index for the separate groups entering on them the various special provisions.

Dr. HUSTEDT thought the mother language should come first and the second language to be the German, French, English etc.

Dr. ROGERS approved Spanish as of equal standing with English, French, German, etc., but opposed relaxation of the requirements of Latin.

Dr. SMITH said if only one language were necessary it might be Japanese, Russian or Chinese etc. He wanted the Latin diagnosis to be imperative.

Prof. PAPENFUSS said he realised that the Latin diagnosis might be extremely short in order to comply with the Rules, and he considered it more or less of a farce.

Prof. HOCHREUTNER: Il est regrettable que la question des langues ait été évoquée. On a admis la diagnose latine à Cambridge et je vous supplie d'en rester là. Si on accepte deux langues vivantes, que pourrions-nous faire si l'on publiait en Chinois ou en Hindoustan?

Mr. STEARN proposed to modify the third line to read "are accompanied by a Latin diagnosis or description," in view of the distinction which had been made by the speakers between a diagnosis and a description.

Dr. A. C. SMITH moved that Art. 38 should be left precisely as it is.

Prof. MERRILL put this to the vote by show of cards.

It was carried by a large majority.

Mr. ROSS then asked if the second part of Prop. 3 could now be considered namely the question of illustrations to accompany algal diagnoses.

Dr. BOIVIN thought this might concern all groups not only Algae.

Dr. HYLANDER proposed postponing this question.

Dr. A. C. SMITH thought no exceptions should be made now.

Prof. PAPENFUSS spoke on the desirability of illustrations as far as Algae were concerned.

Dr. FOSBERG said we cannot legislate good

taxonomic work. We had no reason to believe that the algologists would follow any new rule any more than they have the old. We cannot amend the Rules every time someone makes a mistake.

Dr. BLAKE reverted to the question of compulsory Latin diagnoses for Algae. He stated that the effective date of the requirement for Latin diagnoses had been gradually advanced from 1908 to 1935 because describers (particularly North American ones) of flowering plants had not supplied such diagnoses and suggested that the date for the application of the requirement as regards Algae be moved to Jan. 1st, 1952.

Prof. MERRILL ruled that that matter had already been settled by the vote accepting Art. 38 as it stands.

Dr. SPRAGUE gave a short account of the discussions on the Latin diagnosis at various Congresses. He recalled how Prof. MERRILL had stated at Cambridge in 1930 that he knew no Latin in his youth, but had had no difficulty learning it later in life when he went to the Philippines, and that the late Dr. BRIQUET had added that everyone who had studied the very numerous Latin descriptions of new groups published by Prof. MERRILL knew that they were perfectly clear and intelligible.

Dr. ROGERS said that there was a precedent for the requirement of publication of figures in Art. 45, where the paleobotanists require it. The wishes of the algologists in the matter should be followed.

Dr. DONK said there was a danger in prescribing a description and an illustration because these might be drawn up from different objects. The situation exists already in fossil plants (Art. 45).

Dr. L. O. WILLIAMS said that illustrations are expensive and may sometimes prohibit the publication of a paper on Algae.

Prof. MERRILL then put the following motion before the meeting and called for a vote by show of cards:

"That the last sentence of Art. 38 Prop. 3 (Lund) be added to Art. 38." The vote being

indecisive a vote by *ballot* was taken with the following result:

In favour 150.

Against 174.

PROP. 4 (23: 115) Rejected.

Dr. BLAKE again raised the question of Latin diagnoses of *Algae*. He suggested that the date for the obligatory Latin diagnoses for *Algae* should be moved to Jan. 1st 1953.

Prof. LANJOUW thought it would be unwise to have a special date for algologists.

Prof. PAPENFUSS thought that Dr. BLAKE's proposal would be a satisfactory solution.

Dr. SMITH pointed out that a vote had already been taken on the matter.

Prof. MERRILL ruled that the question had already been settled by the vote in favour of retaining Art. 38 precisely as it stands.

PROP. 5 (18: 207) Rejected.

Article 39

PROP. 1 (6: 194) Rejected.

New Article 39 bis

PROP. (21: 187)

Dr. HYLANDER asked if this proposal of his could be referred to the Special Committee for *Fungi*, as judging from the commentary of the Rapporteur he thought his proposal had been misunderstood.

Prof. MERRILL said the Special Committee on *Fungi* might consider it if they thought fit.

Article 40

PROP. 1 (18: 213) Rejected.

PROP. 2 (27: 199)

Prof. ROUSSEAU asked that this proposal be referred to the Editorial Committee for their consideration.

Prof. MERRILL agreed.

PROP. 3 (20: 128) Rejected.

Article 41

PROP. 1 (7: 148) Rejected.

PROP. 2 (55: 111) Rejected.

PROP. 3 (118: 51)

Dr. SPRAGUE explained that this proposal of Dr. HYLANDER was in two parts, and that the second part concerning fossil plants would come before the Paleobotanical Committee and that it was only necessary to vote on the first part, viz.:

"A name of a taxon is not validly published merely by mention of the subordinated taxa included in it."

He explained the meaning of the proposal saying it referred to such a name as *Rhaptotalaceae* and explained that the name was not validated merely by mention of the three genera included in it. He also pointed out that in Art. 41 as printed in the Synopsis the last word "species" should be replaced by the words "genera; that of a genus is not validated by mention of the included species."

Prof. LANJOUW thought a shorter version could be obtained by replacing Art. 41 by the new Proposal 41 (3) of Dr. HYLANDER, the examples to be included. The whole to be referred to the Editorial Committee.

Prof. MERRILL put this to the vote by show of cards.

It was carried almost unanimously.

Article 42

PROP. 1 (2: 226) Rejected.

PROP. 2 (199: 22)

Dr. DONK said that this proposal would admit names based on descriptions in nurserymen's catalogues.

Dr. HYLANDER pointed out that under the amended version of Art. 36 Prop. 4 which had already been accepted, on and from Jan. 1st 1952, nurserymen's catalogues were not effective means of publication. Descriptions in such catalogues were accompanied by names, and it had been agreed that such names published before Jan. 1st 1952 were effectively

published. Therefore the special difficulty anticipated by Dr. DONK did not arise. The only question for decision was the omission of the words "under another name."

Dr. FOSBERG said he had received from Dr. DONK a carefully written article, and he thought we must be quite clear as to what is meant by "under another name." He thought all the generic names resurrected by O. KUNTZE would have to be accepted if these words were left out.

Dr. SPRAGUE explained his proposal, and said it was to deal with a special case of names which are based on descriptions written before the starting point. Under Art. 42 (2) the generic name *Epipogium* R. Br. was not validly published, since GMELIN had published his description under *Epipogum* an orthographic variant of the same name. If, on the other hand, ROBERT BROWN had proposed an entirely new generic name, that would have been validly published. The omission of the words "under another name" would remove this absurd anomaly.

Dr. FOSBERG asked Dr. SPRAGUE if "name" when used in the Rules means "valid name," or does it mean any name, invalid, vernacular, Pre-Linnean or otherwise?

Dr. SPRAGUE said that the word "name" when used without qualification in the Rules meant simply a name of a taxon. In Art. 42 (2) the name concerned was a "previously and effectively published" one. Pre-Linnean names were not validly published, though they might be effectively published.

Dr. DONK said it was regrettable that the deletion of "under another name" had been proposed because the acceptance would have far-reaching consequences. As the Rules stand now, only new names for already previously named groups are allowed to be published validly by a reference to a previously published description, and more in particular only for the introduction of name changes (isonoms). "Under another name" was introduced at Vienna (1) to get rid of pre-Linnean names (and later on, of pre-starting point names) taken up without an accompanying description; and (2) to

prevent that the mere mention of a name should constitute a valid publication of that older name (O. KUNTZE). With the deletion of these words nomenclators which distinguish between correct names and synonyms will become publications in which numerous new names are validly published and many changes in established nomenclature will have to be accepted. For mycologists especially, STEUDEL's Nomenclator and STREIM's will come to the fore. Long established usage should not be reversed without considering all these consequences more carefully.

Mr. DANDY said he supported Prop. 2 of Dr. SPRAGUE because in his opinion the article would work quite well with the proposed omission. When a name is based on a pre-Linnean name the essential point is that the new name is associated with the description accompanying the earlier name, and whether this earlier name is the same or different from the new one is immaterial. The case of pre-Linnean names revived by OTTO KUNTZE offered no difficulties since they were illegitimate under the Rules.

Dr. ROGERS said that the present Article 20 seemed to cover the situation fully. Mycologists in general find no problem in the deletion proposed.

Dr. HYLANDER asked what was meant by "new" in Art. 38. If a name of a taxon has been effectively but not validly published, is the taxon still a "new" taxon when it is mentioned next time?

Dr. SPRAGUE considered that if the taxon concerned retained the same type and rank it was not "new" when validly published. He thought the wording could be left to the Editorial Committee. He was glad Mr. DANDY had so clearly demonstrated that the new name is associated with the description accompanying the earlier name.

Prof. HOCHREUTNER demande le vote de l'article avec les trois mots supprimés par Mr. SPRAGUE, qui a prouvé qu'il est nécessaire. Cette proposition est acceptée.

Prof. MERRILL put *Art. 42 Prop. 2* to the vote by show of cards.

This was *carried* by a very large majority.

PROP. 3 (0: 197) Rejected.

New Article 42 bis

PROP. (29: 79)

New Article 42 ter

PROP. (25: 78)

Dr. CAMP said that Dr. HYLANDER had withdrawn his *Art. 42 bis* and *ter*, and that he (Dr. CAMP) had proposed a new short article to replace them:

"For purposes of valid publication names in Latin form given to hybrids are subject to the same Rules as those of non-hybrid taxa of corresponding rank."

"Note: The parentage, as far as is known, should be indicated."

Prof. MERRILL put this to the vote by show of cards, and it was *carried* unanimously.

New Article 42 quater

PROP. (24: 77)

Dr. CAMP proposed to modify Dr. HYLANDER's proposal in the following way:

in line 1, to delete the words "or a mixomorph;"

in the Note, to place a full stop after "status," and delete the rest.

Prof. BREMEKAMP asked if there was a definition of the term "nothomorph."

Dr. CAMP said a definition would accompany the first appearance of the word in the Rules.

Prof. BAEHNI asked for an explanation of the term.

Dr. CAMP said nothomorphs are genetic segregates in the same population, they occur in hybrid swarms, they are not geographical races, and have often been described as separate species.

Prof. HOCHREUTNER wished to reject the new proposal, while he feels it is too complicated.

Prof. POLUNIN expressed regret in the interests of simplicity and clarity that it should be deemed necessary to introduce such complicated new terms for what are apt to be the experiences of any botanist who observes species complexes in the field, and consequently wondered whether any useful purpose would be served by introducing the proposed new article.

Prof. MERRILL called for a vote by show of cards on Dr. CAMP's proposal. This was *carried* by a large majority.

As some members of the Section thought the majority was not very large, a re-vote was taken with a count which proved to be 50 in favour and 23 against the Article.

SESSION 8

July 11th, 2—6.10 p. m.

Chairman: T. A. SPRAGUE

Article 43

PROP. 1 (3: 209) Rejected.

PROP. 2 (189: 13) Accepted.

Dr. SPRAGUE explained that the omission of the words "of recent plants" gave the Article a

general application. If the paleobotanists decided against the Article, the text would be varied accordingly by the Editorial Committee.

Art. 43, Prop. 2, was then carried unanimously by show of cards.

PROP. 3 (1: 202) Rejected.

PROP. 4 (175: 41) Accepted.

Dr. BLAKE asked if the effect of this note was merely to validate the specific name involved in a combined generic-specific description. Dr. SPRAGUE replied in the affirmative, and the proposal was unanimously accepted.

New Recommendation XX series

PROP. (199: 31) Accepted.

Dr. SPRAGUE put this to the vote by show of cards and it was *carried* unanimously.

New Article 43 bis

PROP. (22: 22)

This was referred to the Paleobotanical Committee.

New Article 43 ter

PROP. (27: 140)

Dr. HYLANDER asked if this proposal of his could be considered by the Editorial Committee.

Prof. LANJOUW said that this was a case that Dr. SPRAGUE and he had been discussing for two hours without reaching agreement.

Dr. SPRAGUE said that it had been argued (Kew Bull. 1933, pp. 15-18) that *Eragrostis minor* and *E. major* were validly published although the genus *Eragrostis* was not published until three years later. Since opinion might differ as to the interpretation of the Rules in this type of case, he thought that Dr. HYLANDER's new Art. 43 ter was a desirable addition, as it would put an end to controversy.

Prof. LANJOUW agreed that there had been a difference in interpretation but did not think an Article was needed to be added to the Rules merely on that account.

Dr. SPRAGUE recalled that the Article had been accepted by the Utrecht Conference (LANJOUW, Bot. Nomencl. and Tax. p. 40).

Mr. ROSS thought that the question was covered by Art. 45, second sentence. He dis-

agreed with the Rapporteur's comments concerning *Phlyctidia*.

Dr. SPRAGUE then put to the vote by show of cards Dr. HYLANDER's proposal New Art. 43 ter.

This was *carried* by a large majority.

Dr. DONK thought the wording "generic name" insufficient. In the case of a variety, the subspecific or specific name seems to be in question instead of only the generic appellation.

Mr. DANDY asked if the word "*chimaera*" could be left out of Art. 43 ter.

Dr. SPRAGUE thought it might be deleted, and suggested that both Dr. DONK's and Mr. DANDY's proposals be referred to the Editorial Committee.

This was *agreed*.

New Article 43 quater

PROP. (15: 178) Rejected.

New Article 43 quinquies

PROP. (22: 26)

This was referred to the Paleobotanical Committee.

Article 44

PROP. 1 (2: 222) Rejected.

PROP. 2 (204: 20) Accepted.

PROP. 3 (13: 200) Rejected.

PROP. 4 (104: 85) (p. 255 of Synopsis).

Dr. FOSBERG said he could not see why we should distinguish between descriptions of any sort. Why couldn't we have a general recommendation that all taxonomists do careful work?

Prof. HOLTUM said varietal names are often based on very unsatisfactory descriptions, and may be published in works not generally consulted by taxonomists. In horticultural works, such names are sometimes reduced to binomial form by omission of the specific epithets, and such cases, if accompanied by the author's name

or citation of description, might be regarded as publications of new species unless proscribed by rule.

Dr. SPRAGUE thought this new proposal might prove dangerous if it were retroactive. He suggested the addition of "From Jan. 1st 1952."

Mr. DANDY agreed with the proposal as amended, but if it were accepted without amendment the results would be disastrous to nomenclature, as so many specific names have been based on descriptions of taxa of infraspecific rank. Further, it is not clear from the wording whether it is intended to rule out the common practice of raising a variety to specific rank without a change of epithet.

Dr. BOIVIN suggested the proposal be changed to a new Recommendation as follows:

"When a subdivision of a species is raised to specific rank a redescription of the entity should usually be supplied."

Dr. BLAKE stated that the frequent brevity of varietal descriptions is no reason for ruling them out as the bases for specific names, since similarly brief descriptions are accepted as validating specific names.

Prof. BREMEKAMP wished to second Dr. BOIVIN's proposal that it should be made a Recommendation as amended.

Prof. LANJOUW thought it could hardly be used as a Recommendation.

Mr. STEARN said if made retroactive, this proposal would cause numerous changes in nomenclature, as many species have been published in the past simply by raising varieties to specific rank.

Dr. HYLANDER desired to see it an Article with Dr. SPRAGUE's amendment.

Dr. SPRAGUE read out *the proposed Article with his amendment* and then put it to the vote by show of cards.

The vote was indecisive, so a *ballot* was taken.

In favour 168.

Against 181.

New Article 44 bis

PROP. (25: 196) Rejected.

New Article 44 ter

PROP. (15: 19)

Referred to the Paleobotanical Committee.

Article 45

PROP. 1 (3: 210) Rejected.

PROP. 2 (2: 208) Rejected.

PROP. 3 (34: 22)

Referred to the Paleobotanical Committee.

PROP. 4 (193: 6) Accepted.

A vote by show of cards showed *unanimous acceptance*.

PROP. 5 (28: 131) Rejected.

New Article 45 bis

PROP. (19: 192) Rejected.

New Article 45 ter

PROP. (23: 194) Rejected.

Dr. HYLANDER asked if Art. 45 bis and ter could be referred to the Editorial Committee so that his examples should be considered.

Dr. SPRAGUE ruled that that should be done, and thanked Dr. HYLANDER for the great care he had taken in presenting so many useful examples. Those who had examined Dr. Hylander's "Nomenklatorische und Systematische Studien über nordische Gefäßpflanzen" were aware that he had devoted much time and attention to the subject.

Recommendation VIII

At this stage Prof. LAM asked if he might give the Report of the Sub-Committee on the names of higher taxa (Rec. VIII, Prop. 4) and was called upon to do so by the Chairman.

The Sub-Committee consisted of Dr. LE GAL, Mr. ALSTON, Prof. LAM, Prof. MARTIN, Prof. PAPPENFUSS, Dr. ROGERS and Prof. VISCHER.

Prof. LAM explained that it had been decided

to make Rec. VIII, Prop. 4 partly an Article and partly a Recommendation, as follows:

1. Paragraphs (a) and (b) to be adopted as a Recommendation with the following amendments:

That the endings for subdivisions be *-phytina* (instead of *-phytea*), for all groups except Fungi, in which divisions should end in *-mycota*, subdivisions in *-mycotina*.

That in (b) sub 1, first line, the words in parentheses "(or autotrophic *Thallophyta* generally)" be deleted.

That in (b) sub 2, first line, the words in parentheses "(or heterotrophic *Thallophyta* generally)" be deleted.

2. Paragraphs (c) and (f) to be adopted as a new Article, partly replacing Rec. IX.

3. Paragraphs (d) and (e) to be deleted.

Prof. BREMEKAMP pointed out that, if part of the article were to be a Recommendation, it would require slightly different wording.

Prof. LAM said that in (f) although a vote had been given in favour of the substitution of the word "family" by "order," he preferred to keep the word "family."

Dr. ROGERS preferred "family" as there was no provision for conserving names of orders.¹

Dr. SPRAGUE put the following to the vote:

Paragraphs (a) and (b), as amended, to be a Recommendation.

This was carried by a large majority.

The proposal that *paragraph (c) be an Article* was then put to the vote.

This was carried unanimously.

Prof. LAM thought that if (f) were accepted as it stands in the Synopsis, then (d) and (e) could be withdrawn.

Dr. FOSBERG said that if any family could be the type of its order at any author's discretion, there might be a dozen names for each order.

Prof. LANJOUW pointed out that "order" had already been accepted instead of "family" in (f). If "family" is adopted, a list of conserved names of orders will be needed.

¹ This is not true. The meeting accepted for Art. 21 proposal 6 by A. C. SMITH with an amended wording in which is stated that "genera and taxa of a higher rank" may be conserved.—Rapporteur.

Dr. SPRAGUE then put to the vote by show of cards the following:

Those in favour of "family."

Those in favour of "order."

With the result that for family there were 34 in favour, and for "order" 22.

Dr. SPRAGUE asked if a ballot were demanded, to which the Section replied No.

Dr. A. C. SMITH said that the acceptance of this article made a rewording of Art. 21, as revised, necessary. He believed that orders are not now conservable and that the rule of priority does not apply to them.

Dr. SPRAGUE ruled that that would be considered by the Editorial Committee.

At this stage of the proceedings Prof. LANJOUW spoke of the work of the Committee of Typification and a short discussion followed. A mimeographed copy of the findings of the Committee was given to all present.

Dr. DE WIT said that when a substitute type has to be chosen after the holotype has been destroyed (or is irretrievably lost), a duplicate of the holotype (isotype), should have preference above all other possible neotypes.

Prof. LANJOUW considered it was not necessary to discuss this point at this stage, as a second mimeograph copy containing directions for the selection of a neotype was still to follow.

Dr. DE WIT said the second mimeograph is a Recommendation to be followed when a neotype is selected. He wished to enter the point that an isotype should be preferred above all other possible neotypes, into this Article. It is a matter of a Rule not of a Recommendation.

Dr. DE WIT was not supported and the discussion was postponed.

Dr. CAMP asked whether one more point could be cleared up before proceeding with the afternoon's discussion. He referred to § 7 and said his Committee wished to delete the title and substitute "*Names of plants in cultivation.*"

Prof. LANJOUW thought this might form a special chapter.

Dr. CAMP said he would leave that to the

Editorial Committee. He then wrote on the board the new title, and also Art. 35, as amended.

"Art. 35. Plants brought into cultivation from the wild which differ in no fundamental way from the parent stocks bear the same names as are applied to the same species and subdivisions of species in nature.

Plants arising in cultivation through hybridization, mutation, or other processes which tend to establish recognisable differences from the parent stocks receive epithets preferably in common language ("fancy epithets") markedly different from the Latin epithets of species or varieties."

Dr. SPRAGUE called for a vote on the above proposals of the Committee on the Nomenclature of Cultivated Plants.

The voting by show of cards was *almost unanimously in favour*, there being only one dissident.

The Section then resumed its general discussions.

Recommendation XXI

PROP. 1 (112: 71)

This was *accepted* with the addition of the words "if possible" namely: "and 'if possible' where it is preserved."

PROP. 2 (215: 21)

Dr. SPRAGUE asked if one of the American taxonomists would say exactly what was meant by this proposal.

Prof. ST. JOHN said that as far as he could recall he had initiated this proposal of an Article to replace Rec. XXI, which covers the same situation. As a Recommendation it is not binding. Surely it would be helpful to have it obligatory for authors publishing new taxa, to give a precise statement of their taxonomic status.

Dr. FOSBERG said it appears that this proposal is meant to replace only the first paragraph of Rec. XXI. The authors of the proposal approved this point of view.

Dr. CAMP thought it was a compromise.

Dr. SPRAGUE pointed out that Rec. XXI, as it now stood, dealt with two separate matters, the indication of the status of a new group, and the typification of its name. Prop. 1, dealing with typification, had already been accepted.

He then called for a vote on Prop. 2 to replace the first part of Rec. XXI, as an Article, the wording to be amended by the Editorial Committee.

A vote by show of cards in favour of the proposal was *carried* unanimously.

Dr. BOIVIN wished to point out to the Editorial Committee that the word "group" should be changed to "category."

New Recommendation XXII bis

PROP. (167: 50)

"To avoid adoption of names or epithets which have previously been published illegitimately or as *nomina nuda*."

Dr. SPRAGUE said that the new Recommendation dealt with two separate matters, avoiding adoption of names or epithets previously published illegitimately, and avoiding adoption of *nomina nuda*. It would clarify the discussion if these were taken separately. He accordingly proposed the new wording "To avoid adoption of an epithet which has been previously published in an illegitimate combination." He read out the text of Art. 69, the last sentence of which permits the adoption of such epithets. The text now proposed would discourage such adoption.

Dr. FOSBERG said he had intended to include also generic names and all kinds of *nomina nuda*. *Nomina nuda* have often acquired various connotations, so should be forgotten.

Mr. ALSTON thought some examples would be useful.

Dr. SPRAGUE pointed out that there were several examples under Art. 69, but that if Mr. ALSTON had any further examples he should let the Editorial Committee have them.

Dr. SPRAGUE then put to the vote Rec. XXII bis (FOSBERG), as amended above, excluding the reference to *nomina nuda*.

This was *carried* by a very large majority.

The question of *nomina nuda* was then discussed.

Dr. FOSBERG considered that *nomina nuda* should be forgotten rather than given any status.

Mr. ROSS said that if *nomina nuda* include names published with descriptions in modern languages since 1935, following this new recommendation would create chaos.

Dr. SPRAGUE said such names were not *nomina nuda*.

Mr. STEARN said that sometimes plants are widely cultivated in gardens under a particular name before they have been described, and that it was much better in such cases to adopt the name in general currency, rather than propose a new one, an example being *Dahlia coronata*, a name which was retained by Dr. SPRAGUE when he gave a description of the plant as a new species.

Mr. DANDY thought as this is merely a Recommendation and not an Article it would be helpful. Cases such as those mentioned by Mr. ROSS, where it was desirable to adopt names which are technically *nomina nuda* could be dealt with as thought fitting.

Dr. SPRAGUE then called for a vote on Dr. FOSBERG's proposal to avoid the adoption of *nomina nuda*.

This was *carried* by a large majority.

Recommendation XXIII

PROP. 1 (2: 214) Rejected.

Recommendation XXIV

PROP. 1 (203: 10) Accepted.

PROP. 2 (3: 177) Rejected.

Section 7. Citation of Authors' names and of Literature for purposes of Precision

Article 46

PROP. 1 (36: 146) Rejected.

It was decided, however, that this be *referred* to the Editorial Committee.

Article 47

PROP. 1 (188: 22) Accepted.

PROP. 2 (23: 27) Referred to the Paleobotanical Committee.

PROP. 3 (88: 103)

The first paragraph of Prop. 3, which was the same as in Art. 47, had already been considered under Prop. 1.

Prof. LANJOUW suggested that the second paragraph of Prop. 3 should be combined with Art. 47 Prop. 4 (194: 24), which was accepted at the Utrecht Conference, namely, to make the second paragraph of Art. 47 a Recommendation.

Dr. SPRAGUE suggested that this should be *referred* to the Editorial Committee.

By show of cards this was *accepted*.

PROP. 5 (10: 197) Rejected.

New Article 47 bis

PROP. (221: 24)

Prof. LANJOUW pointed out that as this is an Article the word "should" must be changed to "must" in paragraph 2, lines 2 and 4.

Dr. SPRAGUE pointed out that the Note had the nature of a Recommendation and should be treated as such.

Dr. DONEK said that if with "original author" is not meant the "publishing author," this proposition conflicts with Art. 46, which states that the author who first published the name must be indicated.

Dr. SPRAGUE suggested that this proposal (accepted by the preliminary voting) be *referred* to the Editorial Committee for amendment as suggested above.

This was *agreed*.

Article 48

PROP. 1 (21: 443)

PROP. 2 (12: 147)

PROP. 3 (17: 160)

PROP. 4 (59: 108)

PROP. 5 (32: 136)

PROP. 6 (43: 115)

PROP. 7 (34: 113)

PROP. 8 (28: 120)

Prof. LANJOUW pointed out that all these proposals apparently agree with the principle of the first part of this Article. They disagree about the second part. That need not be wondered at, as in that case the second author has himself nothing to do with the new name. The new name appears there only in his Article or Book. He would prefer to take the second paragraph out of the Article and to make it a new Recommendation with the following wording:

"Where a name with a description or reference to a description by one author is published in a work by another author, it is recommended to use the word *in* to connect the names of the two authors."

Dr. BOIVIN expressed his agreement with Prof. LANJOUW's proposal.

Dr. BLAKE pointed out that Proposals 5-8 inclusive were not the same as Proposal 4, and that Prof. LANJOUW's comment did not apply to Prop. 4, which should be considered separately.

Dr. RICKETT said the separation of citations into those in which "*ex*" should be used, and those in which "*in*" should be used implies knowledge often not available as to which author contributed the description. For this reason a semicolon may be substituted for the use of such prepositions. The making of the second half into a Recommendation, leaving the first half as an Article, would make matters even worse. The mutilated Article will often be impossible to follow; it will often be impossible to determine whether the Article or the Recommendation should be applied.

Mr. DANDY thought that the subject under discussion was a matter merely of style; and either that an option, as suggested by Dr. RICKETT, should be permitted, or that the whole subject should be dealt with in a Recommendation rather than an Article.

Dr. SPRAGUE then ruled that a vote should be taken on Prof. LANJOUW's proposal (Syn. pp. 128-9).

A vote by show of cards gave a very considerable majority in favour of the proposal.

Dr. RICKETT spoke on Art. 48 again and proposed the following:

"When a taxon is named by one author but published in the work of a second author, the names of both must be cited. The same holds good for names of garden origin."

Dr. ROGERS said if as proposed the 6th and 7th lines of Art. 48, as printed, are deleted, the option to cite only one author is deleted.

Dr. SPRAGUE called for a vote on Dr. RICKETT's proposal.

A vote by show of cards showed a considerable majority against it.

Dr. SPRAGUE then asked Dr. RICKETT if he would care to have a vote by ballot, to which Dr. RICKETT replied No.

PROP. 4 was then considered.

Dr. BOIVIN said this was a substitution for sentence 3 of the first paragraph of Art. 48.

Dr. SPRAGUE called for a vote by show of cards on Art. 48 Prop. 4.

The result was 21 in favour of the proposal and 32 against.

Article 49

PROP. 1 (170: 62) Accepted.

PROP. 2 (5: 185) Rejected.

PROP. 3 (36: 88)

This was referred to the Editorial Committee.

PROP. 4 (13: 178) Rejected.

New Article 49 bis

PROP. (109: 30) Accepted.

The final word "brackets" to be changed to "parentheses."

New Article 49 ter

PROP. (38: 186) Rejected.

Recommendation XXXPROP. 1 (180: 36) *Accepted.*

Prof. MATTFELD: Statt (Br. for Brown) setze: (R. Br. for Robert Brown; A. Br. for Alexander Braun).

To be referred to the Editorial Committee.

PROP. 2 (102: 66) *Accepted.*

To be referred to the Editorial Committee.

PROP. 3 (13: 187) *Rejected.***Recommendation XXXI**PROP. 1 (17: 204) *Rejected.***New Recommendation XXXI bis**

PROP. (149: 41)

This was referred to the Editorial Committee, to consider the second part only.

Recommendation XXXIIPROP. 1 (5: 197) *Rejected.*PROP. 2 (5: 198) *Rejected.*

Prof. MATTFELD: Vorlinneische Autoren sollen in eckigen Klammern [Tournef.] zitiert werden. Vgl. Internat. Rules Rec. XXXII Examples und die deutsche Fassung des Textes.

Recommendation XXXII terPROP. 1 (30: 143) *Rejected.*

PROP. 2 (78: 100)

PROP. 3 (141: 62)

Dr. RICKETT thought the examples given under Prop. 2 were very clear and should be considered.

Prof. ROBYNS thought Prop. 3 covered Prop. 2.

Dr. RAMSBOTTOM suggested that Prop. 2 should be considered with Prop. 3 and that both should be referred to the Editorial Committee.

Dr. SPRAGUE put this proposal to the vote and it was carried by a very large majority.

Recommendation XXXII quaterPROP. 1 (6: 192) *Rejected.***Recommendation XXXII quinques**

PROP. 1 (86: 91)

PROP. 2 (43: 127)

After a very short discussion which showed that most members were in favour of deleting the recommendation, Dr. SPRAGUE put to the vote the deletion of Rec. XXXII quinques.

This was carried almost unanimously, there being only one against.

Recommendation XXXII septiesPROP. 1 (2: 190) *Rejected.***New Recommendations to follow Rec. XXXII septies**PROP. (2: 214) *Rejected.***Section 3. Retention of names or epithets of groups which are remodelled or divided**PROP. 1 (4: 203) *Rejected.***Article 50**PROP. 1 (214: 12) *Accepted.***New Article 50 bis**PROP. 1 (3: 227) *Rejected.***Article 51**PROP. 1 (2: 223) *Rejected.***Article 52**PROP. 1 (5: 227) *Rejected.***New Article 52 bis**PROP. (2: 226) *Rejected.***New Recommendation to follow Article 52 bis**PROP. (2: 230) *Rejected.***New Article 52 ter**PROP. (3: 228) *Rejected.*

New Article 52 quater

PROP. (3: 226) Rejected.

New Article 52 quinquies

PROP. (3: 226) Rejected.

New Article 52 sexies

PROP. (4: 223) Rejected.

Section 9. Retention of names or epithets of groups below the rank of genus on transference to another genus or species

PROP. 1 (1: 228) Rejected.

PROP. 2 (2: 224) Rejected.

PROP. 3 (14: 210) Rejected.

Article 53

PROP. 1 (85: 130)

There followed a short discussion on this proposal.

Prof. LANJOUW pointed out that the proposal was rejected by the Utrecht Conference, but it was accepted by the American botanists. Against the omission of the words "without change of rank" he saw no objection. He did however, object to "of the same grammatical form." Also he would like to omit the words "of the same rank."

Dr. BLAKE thought that if he read the proposal correctly, thousands of names would have to be changed.

Dr. SPRAGUE thought that the effect of omitting the words "without change of rank" and "of the same rank" would be that we should often have to use *adjectival* names for subgenera, for example in the case of a Series *Plurifoliae* raised to subgeneric rank on transference to another genus.

He then put *Art. 53 Prop. 1* to the vote by show of cards with the result that it was *rejected* almost unanimously.

PROP. 2 (2: 219) Rejected.

PROP. 3 (6: 214) Rejected.

Article 54

PROP. 1 (2: 227) Rejected.

PROP. 2 (12: 199) Rejected.

PROP. 3 (17: 178) Rejected.

Article 55

PROP. 1 (6: 219) Rejected.

PROP. 2 (8: 195) Rejected.

PROP. 3 (14: 201) Rejected.

Dr. SPRAGUE pointed out that the examples given both by Dr. FURTADO and by Dr. HYLANDER under proposals that had been rejected might prove very valuable, and he suggested that the Editorial Committee should be asked to take account of these.

This was agreed.

Section 10. Choice of names when two groups of the same rank are united or in Fungi with a pleomorphic life-cycle

PROP. 1 (15: 89)

PROP. 2 (20: 80)

PROP. 3 (14: 85)

All referred to the special Committees concerned, and to the Editorial Committee.

Article 56

PROP. 1 (153: 51)

Dr. SPRAGUE pointed out that this had nothing to do with the union of two groups, and accordingly did not come under Section 10. *Art. 56, Prop. 1, was then accepted as a separate Article* and referred to the Editorial Committee.

PROP. 2 (2: 216) Rejected.

PROP. 3 (1: 202) Rejected.

PROP. 4 (14: 201) Rejected.

PROP. 5 (137: 76) Accepted.

The wording was referred to the Editorial Committee.

New Article 56 bis

PROP. (29: 163) Rejected.

Recommendation XXXIVPROP. 1 (201: 28) *Accepted.*

Mr. DANDY considered that this proposal, and the Recommendation itself, were now unnecessary in view of New Art. 26 bis (emended) already accepted.

He also proposed the deletion of the words "or sections" from Rec. XXXIV Prop. 1, line 2.

Dr. SPRAGUE asked Mr. AIRY SHAW if he were prepared to delete the words "or sections."

Mr. AIRY SHAW said he would prefer to keep them, but would delete them if the meeting so wished.

This proposal was referred to the Editorial Committee in view of Mr. DANDY's remarks.

PROP. 2 (40: 144)

Dr. BOIVIN withdrew his proposal, as it would be covered by the amendment of Prop. 1 in accordance with Art. 26 bis.

Recommendation XXXVPROP. 1 (10: 150) *Rejected.*PROP. 2 (12: 148) *Withdrawn.*PROP. 3 (20: 132) *Rejected.***Article 57**

PROP. 1 (34: 30)

PROP. 2 (19: 42)

PROP. 3 (16: 56)

All the above were referred to the *Mycological Committee*.

New Article 57 bis

PROP. (31: 19)

Referred to the Paleobotanical Committee.

New Article 57 ter

PROP. (28: 43)

Referred to the Algological Committee.

Section 11. Choice of names when the rank of a group is changedPROP. 1 (2: 188) *Rejected.***Article 58**

PROP. 1 (82: 93)

Postponed until the new Art. 58 bis and Rec. XXXVI had been considered, the final wording of Art. 58 in accordance with subsequent decisions being left to the Editorial Committee.

PROP. 2 (6: 159) *Rejected.*

PROP. 3 (47: 88)

Referred to the Editorial Committee as above.

PROP. 4 (153: 42) *Accepted.*

This was referred to the Editorial Committee as above.

PROP. 5 (113: 61)

This was *accepted* but referred to the Editorial Committee as above.

PROP. 6 (4: 205) *Rejected.***New Article 58 bis**

PROP. (108: 90)

Dr. SPRAGUE ruled that each paragraph should be taken separately.

Paragraph 1. To this he saw no objection, it merely meant that it becomes an Article instead of a Recommendation.

Dr. DONK asked if a taxon of *higher rank* was ever *raised to higher rank*. In the case of a family the family remains what it is and you simply establish in addition to it, a new Order. Compare Art. 10 "every family (belongs) to an Order" the addition appears superfluous.

Prof. ROBYNS thought it would be advisable to change the words "is raised in rank or when the inverse changes occur" into "is changed in rank."

Dr. SPRAGUE said this would be considered by the Editorial Committee.

Dr. SPRAGUE then put *New Art. 58 bis paragraph 1 as an Article* to the vote by show of cards.

This was carried by a large majority.

New Article 58 bis paragraph 2

Dr. BLAKE said if paragraph 2 were adopted it seemed to him that very many generic names would have to be changed.

Dr. DONK thought this was a case of a rule being established at Kew and now proposed to be thrown overboard again. Usage had been solidly established by now, and an ill-considered return on it would be very embarrassing.

Dr. SPRAGUE said that he was not in favour of treating paragraph 2 as an article because it would then become retroactive. He referred to the examples given under Art. 58, and he said that under paragraph 2, but for the conservation of *Wahlenbergia*, that genus would have had to be called *Campanopsis*. There were probably many other cases of generic names

which would have to be changed. The same considerations applied to paragraph 3.

Prof. LANJOUW said that paragraph 1 was the really important part of his and Prof. LAM's proposal, and that they were prepared to withdraw paragraphs 2 and 3.

He proposed to keep Rec. XXXVI, paragraphs 2 and 3, as they stand and to delete paragraph 1.

Prof. HOCHREUTINER then spoke at some length on Rec. XXXVI, he wished to delete the whole recommendation as he felt that it was contrary to the Vienna Rules.

Dr. SPRAGUE pointed out that the first paragraph had already been accepted as a rule.

Prof. HOCHREUTINER propose de supprimer le paragraphe 3 de la Recommandation XXXVI qui a l'air de donner des conseils contre la Règle adoptée à Vienne, qui dit que lors du changement de rang, on doit prendre la plus ancienne combinaison.

Then it was decided to adjourn the discussion till the next session.

SESSION 9

July 17th, 2—6.15 p. m.

Chairman: E. D. MERRILL

Prof. PAPPENFUSS wished to give notice that a representative meeting of algologists attending the Seventh International Botanical Congress wished to record that the action of the Section of Nomenclature in rejecting the principle of Art. 38, Prop. 3, creates such difficulties for algological nomenclature, particularly owing to the large numbers of Algal taxa with diagnoses in a modern language published since 1934, that it will be impossible to obey the Rules strictly and regard these taxa as invalid. It therefore gave notice that proposals to deal with this problem will be laid before the next Congress.

Prof. MERRILL then asked Prof. LANJOUW to speak on the Type Method.

Prof. LANJOUW said that a mimeograph copy recording the decision of the Committee set up

to consider the type method had been handed to each member. The proposals concerned are in Sect. 2 The type method Art. 18—Rec. VII (Synopsis, pp. 20—31).

He explained that a further mimeograph copy would be handed round which contained recommendations for the determination of types. He said the main features from the various proposals had been duly considered, and that the proposals of the Belgian botanists had been most helpful.

He then read out a few corrections to be made on the mimeograph copies.

Prof. MERRILL then informed the meeting that the Special Committee for *Algae* had recommended the rejection of Art. 12, Prop. 2 (Syn. p. 12) and also the new Art 57 ter.

He put a motion for rejection to the vote

and it was *carried* unanimously. Further, the Algological Committee recommended that the decision concerning *Art. 20, Prop. 4* (Syn. p. 34) be *deferred* until the next Congress. This was also put to the vote and *carried* unanimously. The meeting then resumed its discussion on Rec. XXXVI.

Prof. LANJOUW recalled the decisions reached regarding Art. 58 bis and Rec. XXXVI at the last session. Paragraph 1 of Rec. XXXVI to be deleted—it had been accepted as a Rule, and he had proposed to keep paragraphs 2 and 3 as they stood. But Prof. HOCHREUTNER wished to delete paragraph 3.

Prof. MERRILL called on Prof. HOCHREUTNER to speak.

Prof. HOCHREUTNER spoke at some length. He considered the proposal was a contradiction of what was passed at Vienna.

Dr. SPRAGUE replied to Prof. HOCHREUTNER and said there seemed to be a misunderstanding. As far as he could see, there was no contradiction between International Rules ed. 3, Rec. XXXVI paragraph 3, adopted at Cambridge in 1930 and Rec. XXIX, paragraph 3 of the Vienna-Brussels text, as given in Briquet, Rec. Syn., p. 66 (1930). Rec. XXXVI had not been changed at Amsterdam (1935).

Prof. LANJOUW agreed that there was no contradiction and that the proposal was not against the Vienna Rules.

Prof. HOCHREUTNER said it was only a suggestion and that he did not wish to go further.

Prof. MERRILL, asked if he would leave it to the Editorial Committee. He then put to the vote by show of cards that *Rec. XXXVI paragraphs 2 and 3 remain as they are*, but that the Editorial Committee should consider them in the light of Prof. HOCHREUTNER's remarks.

This was *carried* unanimously.

Recommendation XXXVI

PROP. 1	(84: 110)	Withdrawn.
PROP. 2	(2: 222)	Rejected.

Section 12. Rejection of Names.

PROP. 1	(2: 224).	Withdrawn by Prof. HOLTJUM.
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Article 59

PROP. 1	(2: 220)	Rejected.
PROP. 2	(17: 208)	Rejected.
PROP. 3	(176: 50)	Accepted.
PROP. 4	(11: 208)	

Dr. HYLANDER said that his proposal (Art. 59, Prop. 4) included, as an example *Pteretis* which must be solved, and cannot be with the present Rules.

Dr. BOIVIN pointed out that examples given under the proposals of Dr. HYLANDER had been referred to the Editorial Committee.

Prof. MERRILL asked if this could be referred in the same way with a special note concerning *Pteretis*.

Dr. SPRAGUE considered this was a useful case.

Prof. MERRILL asked whether anyone wished to make a motion.

Dr. HYLANDER said he would like it settled as soon as possible.

Dr. FOSBERG suggested that we should include the whole proposition not merely the examples.

Prof. LANJOUW thought the substance of the proposal was given in Art. 60, and that it could not be adopted as a whole. He suggested that in Art. 59 the words "badly chosen" should be replaced by "inappropriate."

Dr. HYLANDER suggested the word "legitimate" should also be put in after the first word "A"—instead of "A name" read "A legitimate name."

Prof. PICHI-SERMOLLI thought the example *Pteretis* was not well chosen for this Article because many authors reject RAFINESQUE's name (*Pteretis*) as *nomen haud recte conditum* and based on *Strupthiopteris* Willd. which is illegitimate.

Dr. BOIVIN said it would be preferable to settle the choice of the name of the genus *Pteretis* sive *Strupthiopteris* sive . . . through the conservation of one of the names.

Prof. ROLLINS moved that Proposal 4 be rejected as by the preliminary voting. This proposition concerns itself only with a special

case and not with the principles of nomenclature for plants as a whole.

Prof. MERRILL moved the *elimination of Prop. 4*, as originally decided. A vote by show of cards to eliminate it was *carried* almost unanimously.

Prof. LANJOUW then asked if the words "legitimate" and inappropriate could be placed in *Art. 59*, to read "*A legitimate name or epithet . . . merely because it is inappropriate . . .*".

Prof. MERRILL put this to the vote and it was *carried* unanimously.

New Article 59 bis

PROP. (21: 146)

Referred to the Horticultural Committee.

Article 60

PROP. 1 (12: 204) Rejected.

Prof. LANJOUW said that this proposal of Dr. WHEELER was rejected by the Utrecht Conference. Dr. HYLANDER, however, had moved to add in the second paragraph of *Art. 60* after "a name" the words "even if validly published." The motion was then carried unanimously at Utrecht. He (Prof. LANJOUW) thought the addition of these words superfluous. He asked if the meeting desired to accept the proposal made at Utrecht, i.e. inserting the words "even if validly published."

Dr. DONK supported by Dr. SPRAGUE considered that the addition of these words was unnecessary in view of *Art. 19*, which states that a name has no status under the Rules unless it is validly published.

Prof. MERRILL asked for a vote by show of cards.

This resulted in 22 in favour and 23 against.

Prof. GOODSPEED thought the meeting was not quite clear as to the position.

After some discussion in which it was pointed out that the example *Tetragonolobus Scandalida* Scop. should be deleted. Prof. MERRILL ruled that *Art. 60, Prop. 1* should be referred to the Editorial Committee as well as the examples.

PROP. 2	(6: 194)	Rejected.
PROP. 3	(10: 182)	Rejected.
PROP. 4	(17: 123)	Rejected.
PROP. 5	(4: 183)	Rejected.
PROP. 6	(2: 185)	Rejected.
PROP. 7	(2: 186)	Rejected.
PROP. 8	(10: 181)	Rejected.
PROP. 9	(16: 194)	Rejected.
PROP. 10	(2: 204)	Rejected.
PROP. 11	(2: 190)	Rejected.
New REC. XXXVI bis (20: 188) Rejected.		

Article 61

PROP. 1	(4: 213)	Rejected.
PROP. 2	(4: 217)	Rejected.
PROP. 3	(14: 196)	Rejected.

Dr. HYLANDER asked whether the Editorial Committee would consider the orthographic variants under *Prop. 3*.

Dr. SPRAGUE considered that would be useful.

Prof. MERRILL ruled that this be so.

PROP. 4 (6: 212) Rejected.

New Article 61 bis

PROP. (28: 158) Rejected.

New Article 61 ter

PROP. (142: 74)

Dr. BOIVIN said it was necessary that the rank of a taxon should be clearly indicated. There must be no uncertainty as to the exact rank to which a name is attached.

Dr. SPRAGUE said he had no objection to the first sentence "a name of a taxonomic group is treated as illegitimate if it was published with alternative ranks." The second sentence might involve too many name changes.

Dr. BLAKE asked whether in the example *Antennaria parvifolia* var. or f. *rosea*, both names would be regarded as illegitimate?

Dr. BOIVIN replied yes.

Prof. MERRILL with Dr. BOIVIN's consent, ruled that the whole proposal should be referred to the next Congress.

New Article 61 quater

PROP. (41: 174) Rejected.

New Article 61 quinquies

PROP. (43: 158)

Dr. COWAN proposed a motion to set up a Committee to consider some means of avoiding changes in the names of cultivated plants of economic importance, and to report to the next Congress.

Prof. LANJOUW said we had had a long discussion on this subject and a ballot, he thought it was hardly necessary to take up the matter again.

Prof. MERRILL agreed, and said the vote was overwhelming.

Mr. GILMOUR seconded Dr. COWAN's motion for the setting up of a Committee to report to the next Congress on the question of the retention of certain widely used illegitimate specific epithets.

Prof. LANJOUW pointed out that a Committee had been appointed at Utrecht to consider this question, and this Committee had come to the conclusion that no *nomina specifica conservanda* should be allowed. He thought it was not necessary to appoint another committee.

Mr. GILMOUR pointed out in reply to Prof. LANJOUW, that the Committee set up at Utrecht had met only once, when four members and five observers were present. At an unofficial vote taken at this meeting the voting was 8 in favour and 5 against a motion "that some means should be adopted to permit the retention of certain illegitimate specific epithets."

Dr. COWAN said he hoped some method would be found to avoid these nomenclature changes, his proposal to set up a Committee was to consider what could be done.

Prof. MERRILL saw no reason against it.

Dr. A. C. SMITH considered that the question had been discussed sufficiently in a former session.

Mrs. SPRAGUE recalled that at Amsterdam in 1935 a Special Committee for the Nomenclature of Economic Plants was set up, of which

she was secretary. It consisted of seven members from various countries in addition to two members whose work it was to supply lists. It was decided that this Committee should publish a list of correct names of economic plants which could be used for ten years. Such a list was proposed so as to enable foresters and horticulturists to find the correct names without too much trouble. The work on this list was started and very good progress was made until the war made it difficult to proceed with it. From experience, however, Mrs. SPRAGUE said it was her view that such a list was not practicable. Although all the members of the Committee worked well, their work was not all of the same standard; the late Dr. EYMA, for instance, made extensive bibliographical researches into almost all names assigned to him for investigation, and must have spent a very large amount of time on the work. To publish such a list with any degree of uniformity was well-nigh impossible unless it was confined to one or two botanists.

The publication of this list was further agreed upon by the horticulturists at the Berlin Horticultural Congress in 1938, subsequently to the rejection of *nomina specifica conservanda* in 1935.

It seems desirable, therefore, that as this list has not, and as far as can be seen, will not materialise, that the horticulturists, foresters and economic botanists should now be granted some form of *nomina specifica rejicienda*, in order, as far as possible, to stabilise the nomenclature of economic plants in the future.

Prof. MERRILL put to the vote by show of cards the proposal that a Committee be appointed to report to the next Congress.

This was rejected by a large majority.

Article 62

PROP. 1 (10: 162)
 PROP. 2 (104: 103)
 PROP. 3 (15: 198)
 PROP. 4 (71: 145)
 PROP. 5 (5: 208)

- PROP. 6 (89: 101)
PROP. 7 (104: 104)

Article 63

- PROP. 1 (29: 181)
PROP. 2 (6: 204)
PROP. 3 (94: 90)

New Article 63 bis

- PROP. (24: 200)

Article 64

- PROP. 1 (4: 197)
PROP. 2 (188: 33)
PROP. 3 (5: 182)
PROP. 4 (29: 60)
PROP. 5 (12: 182)
PROP. 6 (7: 170)
PROP. 7 (18: 188)
PROP. 8 (64: 58)
PROP. 9 (4: 214)
PROP. 10 (127: 78)

As the following discussion embraces Art. 62, 63 and 64, the preliminary voting is recorded above for all the proposals.

- Art. 62 Prop. 1 (10: 162) Rejected.
Art. 62 Prop. 2 (104: 103)

Prof. MERRILL asked Dr. ROTHMALER to speak on this proposal of his and Dr. MANSFELD.

Dr. ROTHMALER: Die ständig in verschiedenem Sinne angewandten Namen müsste man verwerfen können. Es sollte also "owing to segregation" wegfallen; und eine Liste von "*nomina ambigua*" sollte geschaffen werden.

Prof. LANJOUW said he thought the wording in this proposal was an improvement on the wording of the Article, but that he was not in favour of a list of *nomina ambigua*.

Dr. SPRAGUE said that as he and Mrs. Sprague had worked on the case of *Lavandula Spica*, and he considered it to be a "*nomen ambiguum*," he thought it advisable to include the name amongst the examples. He was not how-

ever, in favour of having a list of *nomina ambigua*. He thought each case might be settled on its own merits, perhaps by a permanent bureau of Nomenclature.

Dr. BOIVIN wished to delete Appendix IV and the reference to it in Art. 62.

- Art. 62 Prop. 3 (15: 198) Withdrawn by Dr. HYLANDER.

The discussion continued on Art. 62 dealing with *nomina ambigua*.

Dr. BLAKE said that almost every name had been used with different meanings, and could be regarded as a proper *nomen rejiciendum* as Art. 62 now stands.

Prof. LANJOUW thought that, although it was not necessary to make a list, the article was not superfluous. You can by this Article reject a name which you think has become a permanent source of error.

Dr. A. C. SMITH proposed to delete Arts. 62, 63 and Rec. XXXVII, and to replace them by a new Recommendation to the following effect, the precise wording and the examples to be left to the Editorial Committee. "The names of taxa should be rejected if they are *nomina ambigua*, or *nomina confusa*. When the correct application of such names has been established by subsequent investigation, the name of the author publishing certifying evidence should be cited as well as that of the original author."

Dr. A. C. SMITH had originally suggested that Art. 64 be deleted, but withdrew this proposal when Dr. ROGERS stated that Art. 64 was needed by mycologists, and Mr. ROSS also desired that it should not be deleted.

Prof. LANJOUW thought that the wording "A list of names to be abandoned for this reason (*nomina confusa*) will form Appendix V" should be deleted from Art. 64.

Dr. BOIVIN agreed with this.

Dr. A. C. SMITH considered that there would be no teeth left in the Article if there were no list.

Dr. FOSBERG thought that the words "entirely discordant elements" was subject to much

abuse. It seemed that none of these terms are definable except "*nomen dubium*." He suggested that Art. 62 and 63 and Rec. XXXVII be deleted, and that a Recommendation about *nomina dubia* be adopted. *Nomina dubia* are those names which cannot be typified.

Mr. DANDY said that the three categories under discussion (*nomina confusa*, *nomina dubia*, *nomina ambigua*) are very different. He was in favour of retaining Art. 64 provided that the expression "discordant elements" is made precise by the insertion of some such qualification as "of different families." Art. 63 is superfluous because a *nomen dubium* is inapplicable in any event. He supported Dr. SMITH's proposed Recommendation provided it were restricted to *nomina ambigua*.

Dr. ROGERS said that the Special Committee for *Fungi* recommend the adoption of Art. 64, Prop. 2, and the following modification of Prop. 4 and 8: "For nomenclatural purposes names given to lichens shall be considered as applying to their fungal components, but shall be subject to the provisions of Art. 20 (d)."

Dr. SPRAGUE considered Art. 63 superfluous and wished to see it deleted. Art. 64 was useful and he was glad of the mycologists' support for retaining it. He agreed that the reference to Appendix V should be deleted. He had no objection to Art. 62 provided that the words "owing to segregation" were deleted. He agreed to the deletion of Rec. XXXVII.

Dr. SCHOFF said that, if Dr. SMITH agreed, he would suggest that the Editorial Committee be directed to incorporate the present examples given under present Art. 62, 63 and Rec. XXXVII under the new Recommendation under his motion. Examples are badly needed as an aid to interpretation of these subjective matters.

Dr. HYLANDER seconded Dr. SPRAGUE's proposal and asked for a vote on it.

Dr. FOSBERG asked whose opinion on which names are considered a permanent source of confusion should be sought. Everyone will have his own list.

Prof. PAPENFUSS said, in connection with Art.

64, that it is implied that all taxa based on two discordant elements should be rejected even if it is possible to typify one of the elements, particularly when the diagnosis was largely based on the element with which the taxon has been identified.

Prof. LANJOUW asked whether we should insert "if it cannot be typified."

Dr. ROGERS asked if there could be a vote on the proposal of the Special Committee of *Fungi* given by him.

Dr. SMITH said that in view of what had been said by many speakers he now considered that Art. 64 should not be deleted. He read his proposal over again.

Prof. POLUNIN asked if the attention of the Editorial Committee could be drawn to Art. 62—to replace in line 2, the word "permanent" by "persistent."

Dr. SPRAGUE thought that each Article should be voted upon separately.

Prof. MERRILL ruled that Art. 63 should be voted upon first, and said that the motion was to eliminate Art. 63 and Rec. XXXVII.

Prof. HOCHREUTNER propose de voter séparément sur l'Art. 62 et ensuite sur la liste des "*nomina ambigua*." Il trouve l'article 63 très général et très simple et il comprend, à son avis, les Art. 62 et 64 et la Recommendation XXXVII.

Prof. MERRILL again put the motion before the meeting, to eliminate Art. 63 and Rec. XXXVII.

This was carried by a very large majority.

Prof. MERRILL then put before the meeting that Art. 62 should be eliminated, and replaced by a Recommendation.

Dr. RICKETT felt that Art. 62 should be retained.

Dr. BOIVIN said he liked Dr. SPRAGUE's proposal to delete the words "owing to segregation." He said he would not like to see the example of *Alsine* retained.

Mr. DANDY agreed with Dr. BOIVIN that the example of *Alsine* should be replaced by a more suitable one, or deleted.

Dr. FOSBERG said he objected to placing anything in the Rules which was undefinable, no

two people will apply Arts. 62 and 64 in the same way. We have deleted Art. 63, which was the only one of these Articles which was definable and applicable.

Prof. ST. JOHN said that in his opinion Art. 62 allows the fate of a name to rest on any number of misinterpretations, this would be so, following the sense of the Article, even if it became possible to typify and make clear the application of the original name. He found the effects of Art. 62 bad, and urged its elimination.

Dr. HYLANDER again supported the proposal of Dr. SPRAGUE with regard to Art. 62 (namely to delete the words "owing to segregation").

Prof. LANJOUW suggested that we should have a separate vote on Art. 62 as amended.

Mr. STEARN in support of retaining Art. 62, called attention to the fundamental Art. 4 which states that an essential point in nomenclature is to avoid or to reject the use of forms and names which may cause error or ambiguity or throw science into confusion. Art. 62, as modified, accords with this.

Prof. LANJOUW then asked if there could be a vote on Art. 62 as amended by Drs. MANSFELD, ROTHMALER and SPRAGUE, and he read out the Rule as so amended. He said there would be no list of *nomina ambigua*.¹

Prof. MERRILL put this proposal to the vote and it was carried by a large majority.

The meeting then considered Art. 64.

Dr. ROGERS read out the proposal of the Special Committee for Fungi for the modification of Art. 64, Prop. 4 and 8.

Dr. BOVIN was in favour of this, and proposed the deletion of "a list of names to be abandoned for this reason (*nomina confusa*) will form Appendix V."

Dr. ROGERS agreed.

Dr. BOVIN asked whether we could vote on the new wording proposed by Dr. ROGERS.

Prof. MERRILL ruled that a vote should first

be taken as to whether there should be a list of *nomina confusa*.

A vote by show of cards showed a large majority against the motion.

Prof. MERRILL then asked Mrs. SPRAGUE to read aloud the proposal of Dr. ROGERS, which was as follows:

"A name of a taxonomic group must be rejected if the characters of that group were derived from two or more entirely discordant elements, unless it is possible to select one of these elements as a satisfactory type."

"For nomenclatural purposes names given to lichens shall be considered as applying to their fungal components, but shall be subject to the provisions of Art. 20 (d)."

Prof. MERRILL then put this to the vote by show of cards.

This was carried by a very large majority.

New Article 64 bis

PROP. (26: 194) Rejected.

Article 65

PROP. 1 (59: 169)

PROP. 2 (13: 207) Rejected.

PROP. 3 (15: 207) Rejected.

PROP. 4 (2: 219) Rejected.

The question as to whether this Article 65 should be deleted as proposed in Prop. 1, was considered.

Dr. ROUSSEAU suggested that the word monstrosity should be replaced by some other word, because there is such a case as hereditary monstrosities.

Prof. SCHOFF thought that the examples would illustrate the kind of monstrosity meant.

Prof. MERRILL said he thought they did, and suggested that some additional examples be added.

Mr. STEARN was in favour of retaining the Article.

Prof. LANJOUW thought it might be advisable to retain the Article at least provisionally.

Mr. DANDY pointed out that we did not yet know what the effects would be of deleting Art.

¹ The amended Article reading: A name of a taxonomic group must be rejected if it is used with different meanings, and so becomes a permanent source of error (*nomina ambigua*).

65, as so many garden plants, with names based on them, are monstrosities. He considered that the possible effects of removing the Article should be carefully considered before and at the next Congress. In the meantime he proposed that Art. 65 retained as it is.

Dr. BOIVIN thought the monstrosities should be described so as to make the examples clearer.

Prof. MERRILL put the *proposal of Mr. DANDY to defer action till the next Congress to the vote by show of cards.*

This was *carried* almost unanimously.

New Article 65 bis

PROP. (35: 182) Rejected.

Article 66

PROP. 1 (38: 193) Rejected.

PROP. 2 (2: 229) Rejected.

Article 67

PROP. 1 (16: 205) Rejected.

PROP. 2 (2: 224) Rejected.

Article 68

PROP. 1 (24: 194) Rejected.

Dr. BOIVIN suggested that the examples under Prop. 1 should be added to the examples under Art. 68 as legitimate names.

Prof. MERRILL ruled that these would be *considered by the Editorial Committee.*

PROP. 2 (20: 194) Rejected.

PROP. 3 (198: 39) *Accepted.*

PROP. 4 (9: 207) Rejected.

Mr. ROSS thought it might be well to include the last sentence of Art. 68 Prop. 4.

Dr. SPRAGUE pointed out that this matter would come up later.

PROP. 5 (5: 222) Rejected.

New Article 68 bis

PROP. (163: 47) *Accepted.*

Article 69

PROP. 1 (2: 216) Rejected.

PROP. 2 (174: 53) *Accepted.*

Prof. BAEHNI suggested that an example stating that it is permissible to revive an illegitimate name, if no other one is available. He could, if desired, give a good example.

His offer was accepted on behalf of the Editorial Committee.

PROP. 3 (1: 212) Rejected.

PROP. 4 (101: 89) *Accepted.*

This was *referred to the Editorial Committee.*

PROP. 5 (2: 214) Rejected.

PROP. 6 (35: 179) Rejected.

PROP. 7 (3: 225) Rejected.

Section 13. Orthography of names

PROP. 1 (129: 46) *Accepted.*

PROP. 2 (13: 175) Rejected.

New Article 70

PROP. (24: 193) Rejected.

New Article 71

PROP. (19: 192) Rejected.

New Article 72

PROP. (15: 196) Rejected.

New Article 73

PROP. (21: 186) Rejected.

New Article 74

PROP. (24: 193) Rejected.

New Article 75

PROP. (19: 193) Rejected.

New Article 76

PROP. (20: 192) Rejected.

New Article 77

PROP. (20: 194) Rejected.

New Article 78

PROP. (20: 193) Rejected.

New Article 79

PROP. (17: 194) Rejected.

Although Dr. HYLANDER's new articles had been rejected, it was felt they contained many

valuable suggestions, and it was agreed that the Editorial Committee should consider them from that point of view.

Article 70

PROP. 1	(22: 188)	Rejected.
PROP. 2	(15: 189)	Rejected.
PROP. 3	(8: 197)	Rejected.
PROP. 4	(199: 40)	Accepted.

Prof. POLUNIN drew the attention of the Editorial Committee to the fact that this is an exception to the rule regarding stability of orthography (Art. 70).

Mr. ROSS also drew the attention of the Editorial Committee as to whether this should not cover *-anus*, *-ianus*, and the reverse errors he mentioned, i.e. when we get, hypothetically, *Kernerii* for *Kerneri*. He said he had given Prof. LANJOUW a draft covering all alternatives.

It was agreed that these suggestions of Prof. POLUNIN and Mr. ROSS should be considered by the Editorial Committee.

PROP. 5	(41: 210)	Rejected.
PROP. 6	(201: 49)	Accepted.
PROP. 7	(151: 35)	Accepted.
PROP. 8	(66: 119)	

Dr. SCHOFF proposed the following amended wording of Prop. 8 sentence 2:

"When two or more generic names are so similar, and the plants so closely related, as to cause confusion, they are to be treated as variants of the same name."

Dr. RICKETT said that Prop. 8 was made to legalise present practice as explained in a paper by Dr. SPRAGUE, rather than the confusing provision of the present Art. 70. The wording as amended by Dr. SCHOFF was satisfactory to him.

Prof. MERRILL put to the vote that the whole of Prop. 8 should be referred to the Editorial Committee together with Prop. 4 and Prop. 6.

This was carried.

PROP. 9	(60: 102)	Rejected.
PROP. 10	(5: 171)	Rejected.

New Article 70 bis

PROP.	(44: 169)	Rejected.
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New Article 70 ter

PROP.	(41: 166)	Rejected.
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Recommendation XXXIX

PROP. 1	(182: 13)	Accepted.
PROP. 2	(136: 49)	Accepted.

Prof. MATTFELD: MAGNUS ist ein deutscher Familienname, der nicht als lateinisch oder latinisiert empfunden wird. Eine nach MAGNUS benannte Gattung muss *Magnusia* heissen und nicht etwa *Magnia*. Das Beispiel *Magnusia* after MAGNUS sollte stehen bleiben. Das gleiche gilt für Rec. XL, Prop. 2 (P. 204): eine nach MAGNUS benannte Art muss *Magnusii* heissen und nicht *Magni*. Das Beispiel *Magni* von MAGNUS ist zu streichen. Das Beispiel *Magnusii* ist stehen zu lassen.

Dr. SPRAGUE thought there was a good case for retaining the spelling *Magnusia*.

MAGNUS was a Latin name adopted as a vernacular surname in Sweden and Germany. The generic name formed from this surname in accordance with Rec. XXXIX (b) was therefore *Magnusia* Klotzsch, and the specific epithet was *Magnusii*. DILLENUS, on the other hand, was merely a latinised form of the surname DILLEN, and the generic name and specific epithet derived directly from it, or from the vernacular surname, are therefore *Dillenia* and *Dilleni* respectively. Similarly *Clusia* and *Clusii* were correctly formed from CLUSIUS, since that was merely a latinised form of DE L'ECLUSE.

Dr. RICKETT said MAGNUS might be Latin or not. Therefore the example is confusing.

Prof. MERRILL suggested that Rec. XXXIX, Prop. 2, be referred to the Editorial Committee. This was carried by show of cards.

Prof. LAM asked if the Editorial Committee would also consider the name *Clementis* (from CLEMENS) and add it to the examples.

Prof. MERRILL ruled that these points would also be considered by the Editorial Committee.

Recommendation XL

- PROP. 1 (3: 193)
 PROP. 2 (166: 47) *Accepted.*
 PROP. 3 (36: 134)
 PROP. 4 (27: 164)
 PROP. 5 (69: 101)

Prof. LANJOUW pointed out that these proposals dealt more or less with the same thing and suggested that, although Prop. 2 had been accepted, Props 2-5 be referred to the Editorial Committee.

Prof. POLUNIN said it was desirable to be able to correct original spellings retroactively—which would be especially kind to those working in small institutions where original publications are not available.

Mr. ROSS thought this was already covered.

Prof. MERRILL ruled that all the proposals be sent to the Editorial Committee.

Dr. BLAKE pointed out that in Rec. XLI line 2, the antecedent of the word "these" was evidently "women" and that as it stands the second sentence in the phrase "substantial form" is both unscientific and unchivalrous, unscientific because it puts emphasis on avoirdupois only, unchivalrous because it deprives the more slender members of that division of the human species of the privileges accorded to their stouter sisters. He suggested referring this to the Editorial Committee. (The spelling "substantial" in the Synopsis is a typographical error for "substantival."—Ed.)

Prof. MERRILL said the Editorial Committee must take care of this (laughter).

New Recommendation XLI bis

- PROP. (201: 3) *Accepted.*

Dr. BLAKE wished Rec. XLI bis to be referred to the Editorial Committee to revise the forms of some of the author names used, the form of citation *Ostrya virginiana* (Mill.) Willd. is essentially universal in America.

New. Rec. XLI bis was accepted and referred to the Editorial Committee.

Recommendation XLII

- PROP. 1 (175: 32)

Prof. LANJOUW thought this was a good proposal, as it would be a great help to horticulturists if epithets such as "*silvestris*" and "*sinensis*" were always written in the same way. It would save much time which is now lost in checking the original spelling and it would prevent errors on labels etc.

Dr. SPRAGUE thought it would be undesirable to accept the proposal before we knew the consequences. Botanical Latin was medieval Latin, and he thought the acceptance of the proposal would mean a great many changes in indices etc. He thought a system of cross references would have to be adopted if the proposal were accepted, otherwise an epithet such as "*chinensis*" might be missed if indexed under "*sinensis*."

It would not be wise to take a snap vote.

Mr. STEARN suggested a committee to deal with the subject.

Prof. LANJOUW said they had had a committee before the war, and they had a very large list of such names, and he pointed out that this proposal was only a Recommendation.

Dr. SPRAGUE pointed out that this Recommendation is contrary to Art. 70.

Dr. BOIVIN agreed with Dr. SPRAGUE, and suggested in Art. 70 after the words "original spelling" to insert "except as foreseen under Rec. XLII."

Dr. FOSBERG thought this case was similar to that of *nomina specifica conservanda*. If a list were made there would be no end to it. He moved that we reverse our preliminary vote on Prop. 1.

Dr. ROGERS seconded Dr. FOSBERG's remarks.

Dr. SCHOFF said he also would like to urge that the preliminary vote on Rec. XLII, Prop. 1 be reconsidered. For the sake of stability it seems only practical to follow the original spelling adopted by an author.

Dr. SPRAGUE said if a committee were appointed for approved forms it should be only for the future: we should retain the spelling of an original author.

Dr. LEON said the termination "*ensis*" ought not to be used when applied to a country, but only when it applies to a locality. When the termination applies to a country the termination "*anus*" should be used.

Examples: one may say *havanensis*, but should not say *cubensis* but *cubana* or *cubanus*.

Dr. FRANCO on the suggestion of Dr. PONCE DE LEON to use the termination "*ensis*" for small places and *-anus* for large countries, in the construction of geographical epithets, wished to call attention that this proposal could only apply to epithets formed from countries without old-established names in Latin or Greek form. Paris (Lutetia) is a small place, France (Gallia) is a large place.

Prof. MERRILL felt we could not change old names now.

He moved that the *proposal be sent to the Editorial Committee. This was agreed.*

Recommendation XLII

PROP. 2 (8: 181) Rejected.

Recommendation XLIII

PROP. 1 (103: 102)

PROP. 2 (25: 184)

PROP. 3 (14: 189)

PROP. 4 (55: 152)

PROP. 5 (11: 190)

PROP. 6 (17: 171)

PROP. 7 (2: 212)

Dr. BOIVIN suggested that the decision taken on capitalization or otherwise should be a Rule and not a Recommendation.

Prof. LANJOUW said that this matter must not be mentioned in a Rule as it is relating to typography and not to nomenclature.

Dr. SPRAGUE could not agree with this.

Dr. SMITH thought that due to the negative vote on Art. 70 bis, we could not change Rec. XLIII to a Rule, unless in its present sense.

Dr. ROGERS said the wording of Rec. XLIII in the "Synopsis" differed from that adopted at Amsterdam.

Dr. CAMP said we should be realistic, some

individuals for whom species have been named do not wish to see their names decapitalized; yet various government agencies insist that all specific epithets be decapitalized.

Dr. ROGERS then read a proposal of Dr. GLEASON on decapitalization: "The use of small or capital letters being a matter of typography and not of nomenclature is not subject to the Rules of Nomenclature."

Mr. STEARN agreed with what Dr. CAMP had said.

Prof. MARKGRAF: Unsere Arbeit ist botanisch-taxonomisch; es ist von einem rein praktischen Gesichtspunkt aus unbedingt zu vermeiden, dass ausser dieser botanischen Arbeit auch noch sprachliche Forschungen angestellt werden müssen. Dies wird am leichtesten erreicht durch Vorschrift der Kleinschreibung.

Dr. ROTHMALER: Es ist schwierig festzustellen, ob ein Epitheton klein zu schreiben ist; z. B. wurde erst spät festgestellt, dass das Epitheton von *Vicia lathyroides* einer alten Gattung *Lathyroides* entlehnt ist. Die deutschen Gärtner beschlossen, alle "botanischen" Epitheta mit kleinen Anfangsbuchstaben und die gärtnerischen Namen mit grossen Anfangsbuchstaben zu schreiben.

Dr. BLAKE pointed out that it is impossible to decide by inspection in very many cases whether a given epithet should be capitalized or not, the same epithet being sometimes geographic, sometimes personal, and names identical with generic names sometimes not being generic names.

Prof. BREMEKAMP thought everyone might be free to use capitals as he liked.

Prof. HOCHREUTNER déclare qu'il y a du pour et du contre. Les majuscules donnent une information sur l'origine du nom, ce qui peut être très utile. Il propose de voter pour dire si on est *pour* ou *contre* les majuscules.

Dr. MARTIN recommended the adoption of Prop. 3 amended as follows: "All specific or other epithets may be written with a small initial letter, but those which are derived from the names of persons (substantives or adjectives), or are generic names (substantives or

adjectives, whether in the nominative or in any oblique case) may be capitalized if the author so desires."

Mr. DANDY said that, as had been previously suggested, Rec. XLIII could be deleted, but he thought it would be better to accept a Recommendation on the lines of Prop. 4, so that editors could be shown that it is permissible to spell epithets with small initial letters.

Dr. FOSBERG asked if there could be a vote on Prop. 1 "specific and subspecific epithets should be written with a small initial letter."

Dr. ROGERS wrote a few examples on the board to show how certain specific names so written would appear: *Schinus molle*, *Liriodendron tulipifera*, etc. To those who did not know the origin of the specific epithets it would appear that the gender of the epithet was incorrect.

Prof. MERRILL then put to the vote by ballot Prop. 1.

In favour of decapitalization 212.

Against 129.

Recommendation XLIV

PROP. 1	(18: 175)	Rejected.
PROP. 2	(165: 52)	Accepted.
PROP. 3	(61: 132)	

Dr. RICKETT said that Proposal 3 was made to correct the erroneous statements in Rec. XLIV—the vowels are not "connecting vowels" but terminations of stems. The stems are "albo" "mentha-" "gracili-" "glycy-" etc. Latin stems were in classical usage usually changed to "i," but existing spelling should not be disturbed.

Prof. MERRILL suggested that the Editorial Committee should consider Prop. 3.

Dr. LE GAL said the connecting vowel in Latin may be not only "i" but also "e" and "o." Examples taken from classical Latin authors are "*albogilvus*," "*ahenobarbus*." She hoped the matter could be referred to the Editorial Committee.

Prof. MERRILL put to the vote by show of cards that Prop. 3 be referred to the Editorial Committee. This was carried by a large majority.

Article 71

Dr. HYLANDER asked if his new wording, namely "As to names with varying spelling in LINNAEUS, Species Plantarum, Ed. 1, 1753, or in his Genera Plantarum, Ed. 5, 1754, or names which are differently spelled in these two works, the form used in the list of types of Linnean genera (App. . .) must be adopted" could be used instead of Art. 71.

Prof. LANJOUW apologised to Dr. HYLANDER that his Prop. for Art. 71 was placed under his new Art. 72 (Syn. p. 193) due to the fact that Dr. HYLANDER had so placed it in his own proposals. He thought it was difficult to decide now on Dr. HYLANDER's text.

Dr. BLAKE thought it dangerous to adopt the list as printed, since this point had presumably not been considered when the list was drawn up.

Prof. MERRILL asked if he would like to vote in principle on it. He then put it to the vote by show of cards the following: Art. 71 as it stands or Dr. HYLANDER's proposal 72, 2nd. half on page 193 of the Synopsis. A vote on Dr. HYLANDER's proposal was rejected there being 20 in favour and 29 against.

Art. 71 accordingly remains as it is.

SESSION 10

July 18th, 9.45—11 a. m.

Chairman: T. A. SPRAGUE

Section 14. Gender of Generic Names

Recommendation XLIV his (in place of Art. 72)

PROP. 1	(76: 115)
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Dr. ROTHMALER: Der Vorschlag, alle Art-namen auf das Wort „species“ zu beziehen und

ihnen deshalb eine weibliche Form zu geben, ist schon früher gemacht worden. Die Zoologen schlugen vor, alle Namen (*Epitheta*) männlich zu gebrauchen; die Botaniker dürften alle Namen weiblich gebrauchen. Das ist ein Vorschlag zur Vereinfachung, so wie man schon früher

alle Varietäten und Formen weiblich gebrauchte.

Dr. MATTFELD said that he was strongly in favour of the proposal.

Dr. SCHOFF said he would be in favour of the Article in principle, but suggested that the Editorial Committee be given full latitude in revising the wording of the proposal.

Dr. SPRAGUE did not like the idea of having the ending of the epithet not in agreement with the generic name. He thought it would be unwise that the "outside world" should think that botanists were making mistakes in the gender of their epithets.

Dr. ROUSSEAU thought it was difficult to accept the proposition. In a name like *Astragalus purpureus*, *purpureus* is not the specific name but an epithet—the specific name is *Astragalus purpureus*.

Dr. SPRAGUE put *Rec. XLIV bis Prop. 1* to the vote by show of cards. It was rejected by an overwhelming majority.

PROP. 2 (26: 166)

Dr. BOIVIN thought Dr. HYLANDER's Art. 80 under Prop. 2, might be a valuable asset. He asked what gender should be assigned to *Atriplex*.

Dr. SPRAGUE suggested that he should accept the neuter gender given by Pliny: "*Atriplex et silvestre et sativum est*" (Hist. Nat., ed Harduinus, Vol. 2, p. 221, 1. 4: 1723).

Dr. HYLANDER explained that his Article was aimed at uniformity.

Dr. SPRAGUE suggested that Dr. HYLANDER's Art. 80 should be referred to the Editorial Committee for their consideration.

This was put to the vote and accepted by a very large majority.

New Article 72 bis

PROP. (0: 212) Rejected.

Chapter IV. Interpretation and Modification of the Rules

Article 73

PROP. 1 (11: 119)

PROP. 2 (40: 76)

PROP. 3 (52: 65)

PROP. 4 (40: 82)

Prof. LANJOUW suggested that Arts. 73 and 74, as they do not bear directly on the Rules, should be referred entirely to the Editorial Committee. In view of the decisions reached by the present Congress they have to be thoroughly revised.

Prof. HOCHREUTINER said that the new Art. 28 bis is a definite change in the Rules, which must be accepted now—we must not wait for the next Congress.

Prof. LANJOUW said he hoped the Rules would be published next year.

Dr. SPRAGUE said that all Rules are retroactive, and that with an energetic Rapporteur like Prof. LANJOUW he had no doubt that the Rules would be published next year.

Dr. RAMSBOTTOM said that all our meetings have been on the lines of Art. 74, that is we have been revising the Rules in the light of experience. A new Rule passed at Amsterdam has been considered in this way. There is continuing revision.

Prof. LANJOUW said that nowhere in the Rules are such vague statements to be found as in Arts. 73 and 74 such words as "small Permanent International Executive Committee." What is small? Again, "competent" persons—who is "competent?"

Therefore he thought this part of the Rules would have to be considered very carefully by the Editorial Committee. He thought there should also be some direction as to the distribution of votes.

Prof. LANJOUW went on to speak of committees. He thought instead of the former Executive Committee there should be an *Advisory Board of Nomenclature*—a consultative committee—and he proposed the following as members:

Prof. HOCHREUTINER, Prof. MATTFELD, Prof. MERRILL, Prof. LANJOUW (Rapporteur), Prof. PULLE, Dr. RAMSBOTTOM, Dr. SPRAGUE.

With power to co-opt.

This Committee was unanimously elected.

Prof. LANJOUW then suggested a *General Committee of Botanical Nomenclature* the members to consist of:

All Secretaries of Special Committees as well as Dr. CAMP, Mr. DANDY, Dr. DONK, Prof. HUMBERT, Dr. RICKETT, Prof. ROBYNS, Dr. ROTH-MALER, Prof. VAN STEENIS.

This Committee was unanimously elected. Further special committees were then considered.

Special Committee for Algae:

Secretary: Dr. TORE LEVING.

Dr. BOURELLY (France); Dr. FRANCIS DROUET (U. S. A.); Prof. JEAN FELDMANN (France); Prof. KRIEGER (Germany); Dr. LUND (England); Prof. PAPENFUSS (U. S. A.); Dr. RUTH PATRICK (U. S. A.); Mr. ROSS (England); Prof. O. C. SCHMIDT (Germany); Prof. SKUJA (Sweden); Prof. W. R. TAYLOR (U. S. A.); Prof. VISCHER (Switzerland); Prof. YAMADA (Japan).

Special Committee for Diatomaceae:

Secretary: Mr. ROSS (England).

Mrs. A. CLEVE-EULER (Sweden); Dr. J. FRUGUELLI (S. America); Mr. N. I. HENDEY (England); Dr. F. HUSTEDT (Germany); Dr. R. W. KOLBE (Sweden); Dr. G. KRASSE (Germany); Dr. K. LOHMAN (U. S. A.); Dr. MANGUIN (France); Dr. RUTH PATRICK (U. S. A.); Dr. C. V. SUBRAMANIAN (Madras).

Dr. SPRAGUE first asked for a vote by the algologists which was *carried*. The he asked for a vote from the whole Section on both lists. This was *carried* unanimously.

The Report from the *Paleobotanical Committee* was then considered.

Dr. HAMSHAW THOMAS said the Special Committee for Paleobotany was not informed that the nomination of a new committee was to be made today, and since the matter had only been discussed informally, it was only possible for him to propose the appointment of those paleobotanists who had taken an active part in the work of the Committee in the past, with some additions to make the body more representative. He wished to propose the following:

Prof. HALLE; Prof. FLORIN; Prof. KRÄUSEL;

Prof. JONGMANS; Prof. GOTHAN; Dr. SCHOPF; Prof. ARNOLD; Mr. EDWARDS; Dr. SITHOLEY; and, as temporary secretary, Dr. HAMSHAW THOMAS.

Dr. SCHOPF said that as far as he was aware, the selection of new personnel had not been discussed by the present *Committee on Paleobotany*. This list had certainly not been approved by vote of the present committee. In his opinion it would be well if the Paleobotanical Committee were now completely reorganised. It would be desirable for the *General Committee for Nomenclature* to take this matter under advisement.

Dr. HAMSHAW THOMAS explained that he had put on the list those now serving, and had suggested some new names. The paleobotanists mentioned were certainly needed, perhaps more names should be added. He thought perhaps the Executive Committee might appoint the committee.

Dr. SPRAGUE suggested that it be referred to the *General Committee*, and asked Dr. SCHOPF if he approved.

Dr. SCHOPF agreed.

Dr. SPRAGUE then put that proposal to the vote.

It was *carried* unanimously.

Then followed the proposal of names for the *Special Committee for Fungi*

Dr. G. R. BISBY; Dr. K. B. BOEDIJN; Dr. R. CIFERRI; Dr. M. A. DONK; Dr. C. W. EMMONS; Dr. J. W. GROVES; Prof. R. HEIM; Mr. I. JÖRSTAD; Dr. M. LE GAL; Dr. J. C. LINDQUIST; Prof. W. J. LUTJEHARMS; Prof. G. W. MARTIN; Prof. J. A. NANNFELDT; Dr. J. RAMSBOTTOM; Dr. D. P. ROGERS; Prof. R. SINGER; Mr. J. A. STEVENSON; Dr. A. TROTTER; Miss E. M. WAKEFIELD; Dr. S. P. WILTSHIRE.

With privilege of co-opting additional members.

Prof. ST. JOHN asked who was secretary.

Dr. RAMSBOTTOM proposed Dr. ROGERS.

Miss WAKEFIELD seconded.

Dr. SPRAGUE called for a vote for the election of the above Committee. It was *carried* unanimously.

Special Committee on Nomenclature of Cultivated Plants.

The following names were read out by Dr. CAMP:

Dr. H. H. ALLAN (New Zealand); Dr. B. K. BOOM (Netherlands); Dr. W. H. CAMP (U. S. A.) Dr. J. MACQ. COWAN (Scotland); Dr. H. J. DAEPF (Switzerland); Mr. J. E. DANDY (England); Mr. J. S. L. GILMOUE (England); Dr. N. HYLANDER (Sweden); Prof. G. H. M. LAWRENCE (U. S. A.); Dr. H. W. RICKETT (U. S. A.); Prof. ROLLINS (U. S. A.); Mr. W. T. STEARN (England); Col. F. C. STERN (England).

Other members to be co-opted to cover regional and other interests. When asked who was secretary, Dr. CAMP said this was a delicate question, but for the time being he was acting as temporary secretary.

The Editorial Committee was then considered.

Dr. ROUSSEAU moved the adoption of the following resolution:

I. That the Editorial Committee be empowered:

- 1) To change, if necessary, the wording of any article, and to avoid duplication.
- 2) To add or remove examples.
- 3) To place articles and chapters of the Rules in the most convenient places.
- 4) To place all or part of the recommendations as notes under the proper articles if necessary.
- 5) To change the system of numbering the recommendations for a more convenient one.
- 6) and, in general, to make any editorial modification not affecting the meanings of the provisions concerned.

II. All the delegates are invited to submit their recommendations concerning editorial aspects, and to send them in writing to the

committee before Nov. 1st 1950 (or other date to be determined).

Prof. HOCHREUTNER said the committee has no right to change the sense—he wished to add to the resolution “without changing the sense.”

Dr. SPRAGUE said it was understood that the committee had no right to change the sense of any article or recommendation. They have the power to put the Rules in workmanlike order and to clarify the meaning.

Prof. LANJOUW then read out the proposed names of members of the Editorial Committee:

Prof. BAEHNI, Prof. MATTFELD, Prof. MERRILL, Dr. RICKETT, Prof. ROBYNS, Dr. SPRAGUE. General Editor: Prof. LANJOUW (Rapporteur)

With power to co-opt.

Dr. SPRAGUE asked for a vote on this Committee.

The members were unanimously elected.

Dr. SPRAGUE then called for a vote on the resolutions of Dr. ROUSSEAU. This was carried almost unanimously (one dissentient).

Special Committee for Phanerogams and Pteridophyta.

Prof. LANJOUW stated that it was Mrs. SPRAGUE's wish not to continue being secretary of this committee. He thanked her for all the work she had done in the past and this was applauded by the Section.

The new secretary proposed was Dr. PICH SERMOLLI.

It was proposed to let the General Committee choose the names of this Special Committee and delegates were asked to send in any suggestions. Dr. SPRAGUE put this to the vote and it was carried unanimously.

The meeting adjourned at 11 a. m. At that time all taxonomists joined a special meeting in which the “International Association for Plant Taxonomy” was formed.

SESSION 11

July 18th, 2—5 p. m.

Chairman: T. A. SPRAGUE

Col. STERN remarked that as we heard this morning that an International Association of

Plant Taxonomists had been formed and a Permanent Bureau will be established, he would

like to propose that this Section invites the Permanent Bureau to consider some means of preventing in the future the change of well known names of plants by some method of *nomina specifica rejicienda*. He represented the Royal Horticultural Society of London, who are anxious that some method with this end in view should be adopted, and he had during the last few days met so many users of plant names, foresters, geneticists, plant breeders and horticulturists, and botanists, who are all anxious for this meeting of botanists to find some method of accomplishing this, that he put this proposal before the meeting.

Dr. SPRAGUE pointed out that we had had two ballots dealing with this subject. He realised, however, that it was very important matter for those who were not taxonomists. He saw no objection to referring this proposal to the Permanent Bureau as suggested by Col. STERN, and if so the findings of the Bureau could be brought forward at the next Congress.

Dr. SPRAGUE told Col. STERN that he was perfectly at liberty to send the proposal to the Bureau, and he (Dr. SPRAGUE) thought that this would be better than to ask this Section to go back on their decisions.

Col. STERN agreed to this.

At this juncture Dr. DE WIT suggested that there might be some scientists from Eastern Europe or from Soviet Russia appointed to the committees.

Prof. LANJOUW pointed out that none of these botanists had taken part in the discussions and that all committees had the power of co-option.

Special Committee for Hepaticae

Dr. M. FULFORD, secretary of the Special Committee announced the following resolution:

The Special Committee for Hepaticae suggests the continuation of the present committee with Dr. K. MÜLLER (Freiburg) and Dr. HATORI (Japan) added to it.

Dr. SPRAGUE called for a vote on this.

It was *carried* unanimously.

Special Committee for Musci

Dr. FULFORD explained that a meeting would be held tomorrow evening when the committee would be appointed, and the list would be submitted later.

Dr. SPRAGUE asked the Section if it was content to leave the bryologists to form their own committee the following day. The only thing he thought was for the Section to accept in advance the decision of the bryologists, then if the list did materialize before our next meeting further comments could be made. This was agreed.

The following names were submitted after the final meeting of the Section:

Secretary: Prof. R. VAN DER WIJK (Holland); Dr. E. B. BARTRAM (U. S. A.); Dr. F. DEMARET (Belgium); Dr. H. PERSSON (Sweden); Prof. P. W. RICHARDS (England); Prof. G. SAYRE (U. S. A.); Prof. W. C. STEERE (U. S. A.).

Special Committee for Lichens

Dr. HYLANDER asked if this could be treated in the same way as for Musci. Prof. DU RIETZ wished to resign the position of secretary.

Prof. ROUSSEAU proposed to refer to the General Committee all the questions that had not been discussed by the Section.

Dr. BOIVIN seconded this.

Opinions were divided as to this motion, and no vote was taken.

Dr. SPRAGUE then put to the vote the request of Dr. HYLANDER concerning the Special Committee for Lichens—That it should be treated in the same way as that for Musci.

This was *carried* unanimously.

Dr. SCHOPF then asked if there might now be discussed certain paleobotanical questions.

Dr. SPRAGUE asked Dr. HAMSHAW THOMAS if he wished to make a report.

Dr. HAMSHAW THOMAS in asking for the acceptance of the proposals forwarded by the Special Committee for Paleobotany, it may be stated that the results of the Amsterdam Congress were never widely published and were treated as new proposals for this Congress. The

Special Committee assembled on July 7th and held meetings daily until July 12th.

The following members were present:

Prof. T. G. HALLE; Prof. R. FLORIN, Prof. KRÄUSEL; Prof. W. JONGMANS; Mr. W. N. EDWARDS; Dr. HAMSHAW THOMAS; Dr. SCHOPF; Dr. GOTHAN. In order to make the meetings more representative Prof. C. A. ARNOLD (U. S. A.) and Dr. SITHOLEY (India) were invited to attend. Dr. SELLING of the Naturhistoriska Riksmuseum acted as secretary for the meetings, and Mr. CROFT (British Museum) with Dr. HAMSHAW THOMAS was elected as Chairman.

The different rules and recommendations were very fully considered and the proposals now presented received general agreement. A majority of the committee thought that these rules and recommendations should form a separate appendix, but would, he believed, be prepared to leave this to the Editorial Committee. The main points in the proposals refer to the names of fossil plants which usually were found as detached organs and parts, and need to be given binary names. It was hoped that the rules and recommendations now proposed would cover the various difficulties involved.

As regards the starting date for the names of fossil plants, a majority of the committee wished the fixing of this date to be postponed, pending a full investigation of the changes in established names which might be involved according to whether Jan. 1st or Dec. 31st. 1820 were adopted as the starting date.

Dr. SCHOPF spoke as follows: The special provisions for Paleobotanical Nomenclature now submitted to the Section for Nomenclature are, in my opinion, an immense improvement over the paleobotanical material given consideration at the 1935 Amsterdam Congress. I can recommend their acceptance by this Section. It should be pointed out that the wording may still require much editorial consideration. I believe that the editors will find here a duplication in essence of material already in the Rules, and that the amount of special material can be considerably reduced if the different measures are incorporated in the main body of nomen-

clatural regulations. Many crossreferences in addition will have to be added if this material is placed as an Appendix. I believe there are positive advantages in placing this material in its logical position of reference within the main text, that are quite aside from the extra space required for any other method of handling it.

Editorial attention should also be directed to the words "recent" and "fossil" that have been inserted editorially in the body of Rules at a number of places since the Amsterdam Congress of 1935. These need to be checked very carefully since all these additions by the editor were made with reference to a very different set of special paleobotanical provisions than are now submitted by the committee on paleobotany.

Then followed a short discussion, and Dr. SPRAGUE said he thought if we were not paleobotanists we should be very careful in making suggestions for the alteration of the proposals.

Dr. SCHOPF then spoke on Art. 18 ter. He said we have special nomenclatural provision for fossil plants, but at present there is no indication of just the point at which these provisions become operative, or which of the fossils should be classed according to provisions governing nomenclature of modern groups. This is important because no one doubts that modern species and genera are represented in the fossil state, and he was sure we should all agree that when they can be reliably recognised in the fossil state they should be identified with the proper modern group.

The new Article 18 ter was proposed to relieve this difficulty in deciding which nomenclatural provisions to apply. It seemed reasonable to make the distinction on the basis of whether the type specimen of the taxon was fossil or subfossil, or whether it was modern. He believed that this is a highly satisfactory basis for this nomenclatural distinction.

A question was then asked concerning the position of *Metasequoia*.

Dr. SCHOPF replied that *Metasequoia* is the only genus in which difficulty might arise. At

present there is no other available name for this taxon, so that there is nomenclatural stability. In order not to disturb this desirable condition, he had already proposed, in a written memorandum to the Rapporteur, that the name *Metasequoia Miki* ex Hu and Cheng be conserved with reference to the modern species *M. glyptostrobooides* as type species, rather than with reference to the fragmentary fossil material of *M. disticha* (Heer) Miki as now obtains.

Dr. SPRAGUE wondered whether a paleobotanist might be put on the Editorial Committee.

Dr. SCHOFF suggested the name Dr. NORMAN W. RADFORTH (Mc Master University, Canada). He said that Dr. RADFORTH was well qualified for this work, and at present was serving as representative of the Paleobotanical Section on the Editorial Board of the American Journal of Botany.

Dr. HAMSHAW THOMAS thought this position was a very responsible one, and that perhaps it would be well to have time to consider it.

Dr. SPRAGUE suggested that the Editorial Committee should co-opt a paleobotanical member *if necessary*. He put that to the vote and it was carried unanimously.

The Section then considered certain other proposals in the report.

Dr. SCHOFF spoke on Art. 20, Prop. 7, and said that first things should come first and a primary step in stabilizing fossil plant nomenclature is the date at which nomenclature is taken as legitimate (validly published)—that is the "starting date." At the present time the Rules are ambiguous in this regard. The pertinent sentence in Art. 20, p. 33 of the Synopsis, reads: "The nomenclature of fossil plants of all groups begins with the year 1820."

He had proposed that, in conformity with the other starting dates in Art. 20, this be made to read: "(j) Fossil plants of all groups, Dec. 31st 1820 (STERNBERG, Flora der Vorwelt, Versuch, Fasc. I, pp. 1-24, pls. I-XIII).

This measure is necessary because two important works appeared in the year 1820. The current nomenclature in paleobotany is very

largely that which starts with Sternberg, and it is in fact unthinkable to make the reverse decision and accept the other prominent 1820 publication as a point of departure for legitimate names.

This proposal was widely discussed among American paleobotanists since it was proposed in this form two years ago. It is recognized there that a single publication of definite date *must be selected* before we can set our house in order nomenclaturally.

Surprisingly, however, the Paleobotanical Committee of the present Congress "is unable to accept this proposal because of uncertainty as to the consequences." He supposed unforeseen consequences of adopting the Species Plantarum, May 1753, are still being brought to light.

At any rate he did not presume to foresee all of the consequences that may come from adoption of any rule. The present ambiguous sentence was adopted twenty years ago on recommendations of a number of members of the present committee. There has been no alternative proposal made by the members of the committee in the interval, although at least some members agree that the present Rule is ambiguous. Actually, if we desire regular nomenclature, no other decision is possible than the one proposed here. Most of the useful species names of Schlotheim are validated by later authors. One species name will apparently have to be changed from current usage. The committee has been willing to recommend conservation of one generic name that would otherwise be invalidated. These minor inconveniences are a very small price to pay for a definite starting point in paleobotanical nomenclature. The point the committee fails to recognize is the considerable desirability of making a choice now. If after twenty years study they can advance no better objections it would appear unsound to continue to wait.

Art. 20 is a general rule applying to plants of all groups, and it is in the interests of all botanists that the article be clarified.

Dr. SCHOFF therefore wished to move that Art. 20, Prop. 7 be adopted by a general vote

of the Section of Nomenclature. Any delay in adoption of this proposal will merely serve to postpone the inevitable, and to delay the time at which we can start to use stable nomenclature for fossil plants, those of the Palaeozoic particularly.

Dr. HAMSHAW THOMAS thought this starting point was a very difficult problem and suggested further consideration of it by the committee. He would like to postpone it till the next Congress.

Dr. SCHOFF saw no advantage in waiting five years.

Dr. SPRAGUE thought that this palaeobotanical difficulty could not be adequately dealt with by the Section. The Section was presented with a majority report, and all it could do was to vote upon it.

Prof. LANJOUW suggested voting on the Report first, and to postpone the decision on the starting point.

Dr. RAMSBOTTOM said we had voted on a fixed date. It should only be a Palaeobotanical vote as we have accepted the principle.

Prof. LANJOUW said the palaeobotanists had special pink cards for their voting.

Dr. SPRAGUE suggested a vote by show of pink cards.

Dr. SCHOFF asked for a vote by ballot.

Prof. LANJOUW pointed out that some of the palaeobotanists had not received their cards and suggested a postal ballot, the replies to be sent to him as Rapporteur.

Dr. HAMSHAW THOMAS thought everyone would agree to that.

Dr. SPRAGUE considered that a postal ballot concerning the starting point would be the best solution, and suggested that this ballot should be taken by October.

This was agreed.

Prof. LANJOUW then asked that a vote should now be taken on the Report¹ as the whole (excluding the starting point). He also suggested that the Report be referred to the Editorial Committee.

Dr. SPRAGUE put this to the vote by show of cards and it was carried almost unanimously.

Dr. HYLANDER then asked if he might bring forward part of his proposal 10 of Art. 20, which he had re-worded. He read aloud "If an author accepts and retypes a name published before one of the later starting points mentioned in Art. 20, b, e, f, g, for a genus within such a group, this name shall not be considered a later homonym of the name in its original sense."

Dr. FOSBERG said that names published before the starting point in the group concerned are not validly published, and therefore have no status as earlier names, whether as synonyms or as homonyms.

Dr. ROGERS said that this point had already been dealt with.

Dr. RAMSBOTTOM did not wish to accept Dr. HYLANDER's proposal.

There appeared to be no support for the motion.

The Report of the Special Committee for Fungi² was then considered.

Dr. ROGERS said it was unanimously voted by the Special Committee for Fungi that the attention of the meeting be called to the fact that the adoption of Art. 13, Prop. 1, would not be in the best interests of mycology.

The present Art. 13 which provides that "no classification is admissible which contains such alterations" is harmless, classification not being a matter controlled by the Rules. But the proposed wording "Names given to taxa placed in categories denoted by misplaced terms, are treated as not validly published," would invalidate the principal names of subdivisions of genera in FRIES's "*Systema Mycologicum*." Many of these "tribus" names have been elevated to generic rank, and many others transferred to the rank of subgenera; and many if not most are in universal use by mycologists. To invalidate these names would work a hardship which mycologists would regard as avoidable.

Dr. SPRAGUE suggested that an exception might be made for the names of "*tribes (tribus)*" proposed by FRIES. He asked if there were any further remarks from the mycologists.

¹ See for the accepted report Supplement III.

² See for the accepted report Supplement IV.

Mr. MASON considered that the amended text of Art. 57 proposed by the mycological committee should be rejected on the ground that a state of a species is a category unknown to nomenclature, and that no means of referring to it is being provided.

Miss WAKEFIELD considered that it was sometimes necessary for practical purposes to use the names of imperfect states. She gave the following example of one of the difficulties which arise in compiling lists of fungi if the present Art. 57 is strictly followed: The perfect state of *Actinonema rosae*, described in the United States as *Diplocarpon rosae* Wolf, is not known in Great Britain and it is even possible that if a perfect state were found in Britain it might not be the same as the United States species. Therefore, it is misleading to speak of our fungus as *Diplocarpon rosae*.

Dr. ROGERS said that Art. 57 had not been altered in principle. The application of names to various states has proved indispensable to mycologists. The committee had the benefit of Mr. Mason's discussion and vote in adopting the present text, and a very substantial majority (of which he was not a member) approved it.

Dr. SPRAGUE then put the majority report of the mycological committee to the vote by show of cards, and it was accepted almost unanimously, only one against.

Dr. RAMSBOTTOM then asked if he might propose an amendment to Rec. XLIII, Prop. 1, on decapitalization of specific epithets.

He said that there could be no doubt that whether or not "permission" were given in the amended Rec. XLIII to continue the use of capital initial letters for certain specific epithets, a very substantial proportion of systematists would continue a practice which had been followed for 200 years, which had many advantages for serious students of certain aspects of nomenclature as well as often preventing the perpetration of nomenclatural absurdities. The amendment he proposed was:

"As it was the practice of LINNAEUS and the authors of all the works used as starting points for nomenclature, it is permissible to continue the use of capital initial letters for certain specific epithets."

Prof. MERRILL supported Dr. RAMSBOTTOM's proposal, saying he thought it would clarify the situation.

Dr. FOSBERG said that as Rec. XLIII, Prop. 1, had been accepted by ballot, the matter should be considered as settled.

It was suggested that all such matters might be referred to the General Committee of Nomenclature.

A large majority were in favour of this.

SESSION 12

July 19th, 4.30—6 p. m.

Chairman: E. D. MERRILL

Dr. CAMP gave his final report of the Committee on the Nomenclature of Cultivated Plants.¹ He also placed on the board the following: Insert in Art. 31: "When Latin "specific" names for hybrids are used, all offspring of crossing between individuals of the same parent species receive the same specific name."

Prof. MERRILL put this to the vote by show of cards, and it was unanimously accepted.

Prof. LANJOUW thanked Dr. CAMP for what he had said and for what he had done. It was proposed to establish a new committee to deal with urgent nomenclatural needs. He suggested the committee should consist of the following: Secretary: Prof. LANJOUW.

Dr. CAMP, Mr. DANDY, Dr. GAUSSEN, Mr. GILMOUR, Prof. MERRILL, Prof. SKOTTSBERG, Dr. SPRAGUE and Miss WAKEFIELD.

Prof. MERRILL asked for a formal motion to this effect.

¹ For the whole of the accepted report on § 6 and the Nomenclature of Cultivated Plants see Supplement II.

Dr. SPRAGUE suggested that the terms of reference for the committee should be: "to consider all proposals for reconciling conflicting views on questions of nomenclature held by very large sections of botanists and plant users, and to recommend possible solutions with the least delay."

Mr. SCHWEINFURTH formally proposed this.

Prof. MERRILL put the proposal to the vote by show of cards and it was *carried* unanimously.

Prof. MERRILL then called on Prof. O. N. ALLEN to speak concerning the *Committee for Bacteria*.

Prof. ALLEN said it was very important that a committee for bacteria should be set up, but he was not in a position to name the members. He suggested that Dr. BREED and Dr. S.T. JOHN BROOKS be members and he himself secretary, and that the Congress approve of these Members with powers to co-opt.

Dr. RAMSBOTTOM supported this proposal.

Prof. MERRILL put the motion to the *vote* by show of cards and it was *carried* unanimously.

At this stage Prof. HOCHREUTNER said that as he thought he was the oldest delegate in the assembly, he felt it his duty to thank all the devoted members who had directed and taken part in our discussions, particularly the two presidents, Prof. MERRILL and Dr. SPRAGUE, the Rapporteur, Prof. LANJOUW, the Recorder, Dr. HYLANDER, the three Secretaries Mrs. SPRAGUE, Prof. MATTFELD and Prof. ROBYNS; also Dr. AHLNER, Dr. JONKER, Mr. MENNEGA and Mr. FLORSCHÜTZ.

He wished also to thank all our Swedish friends too numerous to mention. One of them, however, he felt he must name, Prof. R. E. FRIES (Hon. President of the Congress).

Prof. MERRILL expressed the thanks and appreciation of all those mentioned by Prof. HOCHREUTNER.

Prof. LANJOUW then introduced the question of the determination of types.

Part of this discussion had taken place during the session on Monday, July 17th, but it is thought advisable for convenience of reference to record the whole in one place.

A mimeographed copy of proposals entitled "Section 2: The Type Method"¹ was given to each member, and before starting any discussion Prof. LANJOUW drew attention to certain alterations to be made in the mimeograph copy, such as:

Art. 18 bis to read: "The choice of a lectotype or neotype is not binding if the original material is rediscovered, or if it can be shown that the choice was based on misinterpretation of the original description."

Art. 18 ter. Add a note: "Names based on fossil types cannot be used again for modern plants in violation of the Rule excluding later homonyms (see Art. 61)."

Art. 18 quater, paragraph 1 to read: "The nomenclatural type (holotype, lectotype or neotype) of a species or that of a taxon below the rank of species is a single specimen or other element except in the following case. For small herbaceous plants . . . original description."

Cases 2-5 to be renumbered as Notes 1-4.

Prof. LANJOUW explained that all the alterations were considered to be improvements. Prof. MERRILL then asked for any comments.

Dr. BOVIN suggested that Dr. WEATHERBY's recommendation might be added: "When it is necessary to select a nomenclatural type for any group it should be so chosen as to preserve established usage if possible, and typifications by earlier authors should be retained if possible."

Prof. LANJOUW replied that the guide for the determination of types would be given later in a mimeograph copy, and that discussion had better be postponed till then.

Mr. ROSS thought the words in Art. 18 quater "of each" in Note 4, originally 5, seemed unnecessary, and their inclusion made the note confusing. They should be deleted. The retention of them would give the note a different effect from that intended.

Dr. SPRAGUE agreed, and suggested that the final "of" be replaced by "in." Note 4, to read as follows: "If a taxon included subordinate

¹ The complete text accepted by the Congress at the end of this report in Supplement I.

taxa its type must be or include the type of one of the taxa in each subordinate rank."

Dr. SCHOFF replied concerning the types of names of fossil plants.

Prof. MERRILL suggested that this be left to the Editorial Committee.

Prof. BAEHNI asked what was the position of *Metasequoia*.

Dr. SCHOFF said that at present there was only one generic name for the fossil and for the recent plant. If some botanist proposed a new name, *Metasequoia* could be conserved.

Prof. LANJOUW said that he had a proposal for the conservation of the name *Metasequoia*.

Dr. DE WIT wished the following changes to be made on p. 1: After the sentence: "The substitute may be either a *lectotype* or a *neotype*" add: "When choosing, the isotype has preference over all other possible lectotypes." He considered that this provision should be in an Article, not a Recommendation.

He further proposed that the sentence (1. 8 from bottom) which reads: "An isotype is a specimen believed to be a duplicate of the holotype" should be replaced by "An isotype is a duplicate of the holotype."

Prof. LANJOUW thought it was not necessary to discuss this point at this stage, it would be better to wait for the Guide for the Determination of Types.

Prof. MERRILL ruled that this be so.

Dr. RUTH PATRICK pointed out to the Editorial Committee that Art. 18, Note 3, paragraph 5 should be placed before paragraph 4.

Prof. MERRILL proposed that the matter be referred to the Editorial Committee.

This was carried unanimously.

A mimeographed copy of the "Guide for the determination of types" was then distributed.

Prof. MERRILL called on Dr. FOSBERG to speak.

Dr. FOSBERG said that the suggestions put forward are presented as a means of applying the Articles concerning the type method. These also include certain matters of good taxonomic practice.

Dr. BOIVIN proposed that we should add to

(4) "Whenever the type material of a taxon is heterogeneous, the lectotype should be selected so as to preserve current usage if possible."

Ex.: The syntypes of *Thalictrum dioicum* L. include one specimen of what is currently called *T. dioicum* L. and one of *T. polygamum* Muhl. The first specimen was properly selected as lectotype in 1944, thus preserving current usage.

Prof. LANJOUW thought this might be an useful addition.

Dr. FOSBERG said that this point was deliberately omitted as it might conflict with the author's intent.

Prof. LANJOUW pointed out that the proposal said "if possible," so perhaps it could be accepted.

Prof. MERRILL asked whether it could be submitted to the Editorial Committee.

Dr. FOSBERG agreed.

Dr. DE WIT proposed that to Art. 18, centre of page, after the sentence "A substitute may be either a lectotype or a neotype" should be added: "When choosing, the isotype has preference above all other possible lectotypes." He went on to say that it could not be maintained that Art. 18 explains the type method, and the Recommendation the manner of determining a type.

In Art. 18 there is also prescribed "a lectotype always takes precedence over a neotype" which is a direction for choosing. His proposal was that an isotype, because it forms part of the type *sensu latiore*, must have precedence over all other possible types. It is a matter for an Article, not for a Recommendation which may be followed or not. The further designation of neotypes may, indeed, be referred to a Recommendation.

A second point was that in the final part of Art. 18 an improvement in the text is necessary. It reads: "An isotype is a specimen believed to be a duplicate of the holotype." This he pointed out was wrong. What a specimen is *believed* to be is irrelevant. When he believed a specimen to be a duplicate, that does not make it a duplicate: The text should be "An isotype is a duplicate of the holotype."

After a short discussion Dr. FOSBERG said that the reason that the matter of requiring selection of an isotype as lectotype was omitted was that often the author has not seen all the isotypes. It is much better to permit selection of a paratype if the author has seen it.

Prof. LANJOUW said he hoped this matter would be left to the Editorial Committee.

Prof. MERRILL proposed that this be sent to the Editorial Committee to incorporate such suggestions as they consider necessary, and this was *carried* unanimously.

Prof. HOCHREUTINER suggested that it should be made as simple as possible.

Prof. LANJOUW then asked if we could vote on the Guide as given by Dr. FOSBERG, and that it should be sent to the Editorial Committee.

Dr. BOIVIN seconded.

Prof. MERRILL put Prof. LANJOUW's proposal to the vote and it was *carried* unanimously.

Prof. MERRILL then announced that a proposal for the *Special Committee for Lichenes* had been submitted. The following names were suggested:

Secretary: Dr. S. AHLNER (Sweden); Prof. H. DES ABBAYES (France); Dr. C. W. DODGE (U. S. A.); Dr. V. J. GRUMMAN (Germany); Dr. J. MACKENZIE LAMB (Canada); Dr. J. MOTYKA; Dr. R. A. MAAS GEESTERANUS (Holland); Mr. R. SANTESSON (Sweden).

Prof. MERRILL put these names to the vote, and they were unanimously *elected*.

Appendix I. Regulations for determining types

- PROP. 1 (33: 80)
- PROP. 2 (24: 81)
- PROP. 3 (2: 92)

This Prof. LANJOUW pointed out had already been dealt with.

Appendix II. Nomina Familiarum Conservanda

- PROP. 1 (82: 48)
- PROP. 2 (81: 41)
- PROP. 3 (95: 38)
- PROP. 4 (85: 44)

Prof. LANJOUW proposed that Appendix II be referred to the *Special Committees* concerned with acting power.

Dr. BOIVIN seconded.

Prof. MERRILL put this proposal to the vote and it was *carried* unanimously.

Appendix III. Nomina Generica Conservanda

Prof. LANJOUW proposed that these *nomina generica conservanda* should be dealt with by the various *Special Committees* concerned, and that the committees be given acting power.

Dr. RUTH PATRICK urged that the Congress should issue a general policy concerning *nomina generica conservanda*, some wish to conserve names of genera which have only a few species in them, this should not be done unless there is an economic reason, or other special reason for so doing.

Prof. LANJOUW agreed with this and thought it might be discussed in the General Committee for Nomenclature.

Dr. FOSBERG wished to emphasize Dr. RUTH PATRICK's remarks. It seemed to him that hundreds of names had been proposed in recent years for conservation of names of groups of no imaginable economic or general importance. It had taken 45 years to get a relatively small list in final shape. What will be the result of the present flood of proposals.

Dr. SPRAGUE told the meeting how he had prepared lists of proposed names for conservation both for the Cambridge congress and for the Amsterdam congress. He said what a long time it took to prepare cases and that a name was never put forward unless there was good reason for its conservation.

Mrs. SPRAGUE explained that the lists put forward after the Cambridge congress were large because there had been a change in the homonym rule at that Congress. It was felt that this change might give rise to a great number of generic name changes unless there was fairly wide conservation. Accordingly the late Dr. HITCHCOCK and Dr. WEATHERBY and she herself were asked to work through the generic homonyms and to propose for conser-

vation those names which they thought ought to be conserved. This was done, with the result that some 400 names were later conserved. This was of course a very special case.

Prof. LANJOUW then submitted the names proposed for the *Special Committee for Pteridophyta*.

Secretary: Prof. R. PICI-SERMOLLI (Italy); Mr. ALSTON (England); Dr. MORTON (U. S. A.); Prof. HOLTUM (Singapore); Mr. BALLARD (England); Mme. TARDIEU BLOT (France); Dr. COPELAND (U.S.A.)

This list was then put to the vote and carried unanimously.

Dr. ROGERS asked what was the power of the Special Committee with regard to *nomina conservanda proposita*.

Prof. MERRILL said they had power to conserve.

Prof. LANJOUW thought they would refer to the General Committee.

Dr. SPRAGUE said in the last Congress these committees had been given power, and they had worked in some cases exceedingly well, especially where the committee had an energetic secretary. He suggested power be given to the committee and then it should secure the sanction of the General Committee for conservation.

Prof. BAEHNI asked how we were to know what names were conserved.

Prof. LANJOUW asked if he meant between the Congresses.

Prof. BAEHNI: Yes.

Prof. LANJOUW: By means of our new association we will publish new lists as soon as they are available.

Dr. BLAKE inquired whether the list of proposed *nomina generica conservanda* would be published in a preliminary way so that the names would be subject to criticism before final adoption.

Dr. RAMSBOTTOM replied that the names would be accepted informally in the interim, the list to be tentative until formally approved by the next Congress.

Dr. ROGERS said he agreed to that.

Mr. ROSS urged that the secretaries of the

Special Committees should be instructed to obtain the approval of relevant other committees where the names to be rejected fall outside the purview of their own committee.

Prof. LANJOUW explained that this had always been done.

Dr. FOSBERG suggested that when the names are referred to the Special Committees, a set of instructions to be prepared by Dr. SPRAGUE on principles for selection of names for conservation be referred to the committees at the same time.

Dr. SPRAGUE agreed to prepare a set of instructions as Dr. FOSBERG had suggested, and to send it to the Rapporteur.¹

Prof. MERRILL put the motion before the meeting that *Committees have power to select names for conservation* but the list will be tentative until the next Congress.

This was carried by a large majority.

Mr. STEARN asked for means whereby a decision of the Committee on *Nomina Generica Conservanda* could be made known as quickly as possible. Compilers of encyclopaedias and other users of names naturally desire to learn whether a name is to be preserved or not, at the earliest opportunity, so that their works may not become too soon antiquated.

Prof. LANJOUW said that committees could publish their lists as soon as they had made them, but it was not possible at this stage to say how long a particular committee might be in producing a list.

The names proposed for the *Committee of Phanerogamae* were then read out by Prof. LANJOUW.

Secretary: Prof. PICI-SERMOLLI (Italy); Prof. LAM (Holland); Prof. MANSFELD (Germany); Prof. HOCHREUTINER (Switzerland); Dr. RICKETT (U. S. A.); Dr. A. C. SMITH (U. S. A.); Prof. WEIMARCK (Sweden); Mr. DANDY (England); Mr. PINTO DA SILVA (Portugal); Dr. LEANDRI (France); Prof. VAN STEENIS (Holland); Dr. FOSBERG (U. S. A.).

¹ Soon after the Congress this set of instructions was prepared by Dr. SPRAGUE, and published in "Taxon", Vol. I, p. 14.

Prof. MERRILL put these names to the vote and they were unanimously *elected*.

Appendix IV. Nomina ambigua

Deleted.

Appendix V. Nomina confusa

Deleted.

Appendix VII. Nomenclature of Garden Plants

PROP. 1 (2: 73)

PROP. 2 (4: 77)

PROP. 3 (71: 9)

This matter had already been dealt with.

New Appendix VIII. Special Provisions concerning Fossil Plants

PROP. 1 (22: 26)

PROP. 2 (24: 29)

This also had been dealt with.

New Appendix (Syn. p. 249). Nomina excludenda

PROP. 1 (28: 146)

This also had already been dealt with.

New Appendix (Syn. p. 250). Rules for Citation

PROP. 1 (149: 22) *Accepted.*

Prof. LANJOUW pointed out that Dr. RICKETT was a member of the Editorial Committee, so we need not worry too much over this new Appendix. To this the meeting *agreed*.

Supplementum: Species Lectotypicae propositae

Prof. LANJOUW considered this was a very difficult matter, and thought it could only be judged by the Special Committees concerned.

Dr. BOVIN felt that we should not have such lists in our Rules, with the possible exception of the Linnean list.

Dr. FOSBERG said he saw no end to such lists. It seems best to assume that workers will be sufficiently familiar with the literature of their groups to know what lectotypes have been suggested without compiling a compendium to help them.

Prof. MERRILL pointed out that the first list in the Synopsis proposed lectotypes for *Nomina Generica* adopted at the Cambridge and Amsterdam congresses.

Dr. SPRAGUE explained that the list of lectotypes for the Linnean genera compiled by HITCHCOCK and M. L. SPRAGUE was accepted subject to revision if necessary by those familiar with special groups. He thought the present lists might be accepted in the same way. For the final list we must consider the work of the monographer.

The Section seemed to approve of the above discussion, and no vote was taken.

Dr. RAMSBOTTOM then asked if he might speak on decapitalization of specific epithets. He thought there had been misunderstanding, and asked if there could be a ballot.

Prof. POLUNIN said we had already had a ballot on this issue, and decapitalization was recommended.

Dr. RAMSBOTTOM said that he considered there ought to be an amendment to allow those botanists who had consistently followed the Rules and Recommendations all these years to retain the capital initial letter in certain specific epithets. If the Recommendation remained as it now stands, it would not be followed. He read out his proposed amendment:

"As it was the practice of Linnaeus and the authors of all the works used as starting points for nomenclature, it is permissible to continue the use of capital initial letters for certain specific epithets."

Dr. BOVIN suggested this should be submitted to the Editorial Committee.

Prof. POLUNIN still thought we should consider the matter settled. He failed to see why Dr. RAMSBOTTOM's proposal, which was exactly the same as the proposal he had suggested (Rec. XLIII, prop. 6) and which was rejected in the preliminary voting (17: 171) should be accepted instead.

Dr. ROGERS thought something might be done to allow those who wished to capitalize to do so.

Dr. SPRAGUE asked if he might read out Prof. POLUNIN's proposal Rec. XLIII, Prop. 6:

Modify as follows: "All specific and trivial names and epithets should be written with a small initial letter, although writers desiring to use capital initial letters for particular names or epithets may do so when these are directly derived from names of persons (or deities) or vernacular (or barbaric) names, or are previously published (including pre-Linnean and invalid) unmodified generic names."

Dr. SPRAGUE then proposed that this be accepted.

Prof. POLUNIN said he appeared to have a foot in both camps.

Dr. SINGER did not care for the word "unmodified."

Prof. MERRILL gave as an example *Gluta Renghas*, this was by error published by Linnaeus as *Gluta Benghas*. The Malay name is *Renghas*.

Prof. MERRILL then put the following motion before the Section:

"To substitute POLUNIN, Prop. 6, subject to modification by the Editorial Committee, instead of what we have adopted."

A vote by show of cards was taken and the proposal was *accepted* by a very large majority.

Prof. POLUNIN asked that the Editorial Committee should reword in two places in accordance with his reprint p. 222, that is, insert "especially" before "desire" and substitute "whether actual or mythical" for "or deities."

Dr. SPRAGUE then put before the Section the *formal motion* to be put forward at the Final Plenary Meeting of the Congress:

"That the Seventh International Botanical Congress accepts the decisions of the Section of Nomenclature concerning the modification of the International Rules of Botanical Nomenclature, and sanctions the appointment of the Standing Committees by this Section."

Prof. MERRILL then thanked all for the support given during the discussions, and declared the proceedings closed.

SUPPLEMENT I

Section 2, The Type Method

Article 18

The application of names of taxa is determined by means of *nomenclatural types*. A nomenclatural type (*typus*) is that constituent element of a taxon to which the name of the taxon is permanently attached, whether as an accepted name or a synonym. The name of a taxon must be changed if the type of the name is excluded (see Art. 66).

Note 1: The nomenclatural type is not necessarily the most typical or representative element of a taxon; it is merely that element with which the name is permanently associated.

Note 2: A *holotype* ("type") is the one specimen or other element used by the author or designated by him as the nomenclatural type

(that is, the element to which the name of the taxon is permanently attached).

Note 3: If no holotype has been indicated by the author who described a taxon, or when the holotype is lost or destroyed, a substitute for it must be chosen. The author who makes this choice must be followed unless it can be proved that the choice was not made in accordance with Art. 18 bis. The substitute may be either a *lectotype* or a *neotype*. A lectotype always takes precedence over a neotype.

A *lectotype* is a specimen or other element selected from the *original material* to serve as nomenclatural type when the *holotype* ("type") was not designated at the time of publication, or so long as it is missing.

When two or more specimens have been designated as types by the author of a name (e.g. male and female, flowering and fruiting, etc.) one of them must be chosen as lectotype.

A *neotype* is a specimen selected to serve as nomenclatural type so long as all of the material on which the name of the taxon was based is missing.

Recommendation

For other specimens of special interest the following terms are recommended:

A *paratype* is a specimen cited with the original description other than the holotype. An *isotype* is a specimen believed to be a duplicate of the holotype. A *syntype* is one of two or more specimens or elements used by the author when no holotype was designated, or one of two or more specimens simultaneously designated as type.

Recommendation

It cannot be too strongly recommended that the original material, especially the holotype, of a taxon be deposited in a permanent responsible institution and that it be scrupulously cared for and preserved. When living material has been designated as type, it should be immediately preserved, whether it be a living plant in garden or greenhouse, or a culture in vitro.

Article 18 bis

The choice of a *lectotype* or *neotype* is not binding if the original material is rediscovered, or if it can be shown that the choice was based on a misinterpretation of the original description.

Article 18 ter

Names based on types derived from modern material, *Algae* excepted, always take precedence over names based on fossil or sub-fossil specimens.

Note: Names based on fossil types cannot be

used again for modern plants in violation of the rule excluding later homonyms (see Art. 61).

Article 18 quater

The nomenclatural type (holotype, lectotype or neotype) of a species or taxon below the rank of species is a single specimen or other element except in the following case:

For small herbaceous plants and for most non-vascular plants the type may consist of more than one individual, which ought to be conserved permanently and assembled on one herbarium sheet or preparation.

If it is proved later that such a type herbarium sheet or preparation contains parts belonging to more than one taxon, the name must remain attached to that part (lectotype) which corresponds most nearly with the original description.

Notes:

- 1) For plants for which it is impossible to preserve a type specimen, the type may be a figure and/or a description.
- 2) In a species without a type specimen, the type may be a description or figure.
- 3) If a taxon is divided into a number of taxa of the same rank, the nomenclatural type of the original taxon must be the type of one of them.
- 4) If a taxon includes subordinate taxa, its type must be or include the type of one of the taxa in each subordinate rank.

Article 18 quinquies

The nomenclatural type of an order and of taxa between order and family is a family, that of a family and of taxa between family and genus is a genus, and that of a genus and of taxa between genus and species is a species.

The nomenclatural type of a taxon above the rank of genus, to the rank of order, whose name is formed in accordance with the Rules, is always the lower taxon whose name was derived from the same root (generic name).

Note: It is not felt that the type method can, at present, be profitably applied to the nomenclature of taxa above the rank of order.

Recommendation

Guide for the determination of types

The following set of suggestions is intended both as a guide to the application of the Rules and as an indication of sound practice in the determination or selection of the nomenclatural types of previously published taxa.

Where the application of a rule is embodied in a suggestion, reference is made to the appropriate article.

1) The choice of the original author, if definitely expressed at the time of the original publication of the name of the taxon, is final. If he included only one element, that one must always be accepted as the holotype (see Arts. 18, 18 quater). If a new name is based on a previously published description of the taxon, the same considerations apply to material cited by the earlier author.

2) When a new name was published as an avowed substitute (*nomen novum*) for an older one (a new name based on the description accompanying an illegitimate or incorrect one), the type of the new one is automatically that of the old one.

3) A lectotype may be chosen only when an author failed to designate a holotype, or when, in species or taxa of lower rank, the type has been lost or destroyed (Art. 18 note 3).

4) Designation of a lectotype should only be undertaken in the light of an understanding of the group concerned. Mechanical systems, such as the automatic selection of the first species or specimen cited or of a specimen collected by the person after whom a species is named, should be avoided as unscientific and productive of possible future confusion and further change. The original description of the taxon concerned should be the basic guide (Art. 18 bis).

a) In choosing a lectotype any indication of intent by the author of a name should be given preference unless it is contrary to his description and remarks. Such indications are manuscript notes, annotations on herbarium sheets, recognizable figures, epithets such as *typicus*, *genuinus*, *vulgaris*, *communis*, etc.

b) A lectotype must be chosen from among

elements that were definitely studied by the author up to the time the taxon was published and included in it when it was published (Art. 18 note 3).

c) Other things being equal, specimens should be given preference over pre-Linnean or other cited descriptions or plates when designating lectotypes of species.

d) In cases where two or more elements were included in or cited with the original description the reviewer must use his own judgment in selection of a lectotype, but if another author has already segregated out one or more elements as other taxa, the residue or part of it should be designated as the type if its essential characters correspond to the original description. If it can be shown that the element best fitting the whole published original account has been removed, it shall be restored and treated as lectotype (Art. 18 bis). Whenever the type material of a taxon is heterogeneous the lectotype should be selected so as to preserve current usage if possible. (Ed. Comm.)

e) The first choice of a lectotype should be followed by subsequent workers unless it can be shown that the choice does not fit the original description as well as another of the original elements (specimens, species, higher taxa, etc.). (Art. 18 bis.)

5) In selecting a *neotype* even more care and critical knowledge are essential, as the reviewer has usually no guide except his own judgment as to what best fits the original description. If his selection is faulty it will inevitably result in further change. The neotype may only be selected when all original material is believed lost or destroyed (Art. 18 note 3, Art. 18 ter).

6) For names of fossil species the lectotype where one is needed should, if possible, be a specimen illustrated at the time of the first valid publication.

7) The nomenclatural typification of organ genera, form genera, of genera based on plant microfossils (pollen, spores, etc.), genera of imperfect fungi, or any other analogous genera, or lower taxa, does not differ from that recommended above.

SUPPLEMENT II

Summary of Proposals by "Committee on Nomenclature of Cultivated Plants" as accepted by the Congress

§ 6. Names of hybrids and some other special categories

Article 31

(Prop. 7—accepted with following modifications)

"Hybrids or putative hybrids between two species of . . ." etc.

(3rd paragraph, line 2).

"is distinguished from the latter by the sign × before the binary ("specific") epithet."

Examples: (consult Mr. STEARN).

Insert in this article: "When Latin "specific" names for hybrids are used, all offspring of crossing between individuals of the same species receive the same specific name."

"Note 1: (line 2, next to last word), change "will" to "may."

Article 31 bis

(New text).

Hybrids or putative hybrids between infraspecific taxa of the same species may be designated by a formula and, wherever it seems useful or necessary, by a name of the same taxonomic rank as the parents or, if these are of different rank, that of the higher ranking parent. In the formula the order of the epithets and the use of — — (continue to end of proposed text).

Examples: (to be supplied by Mr. STEARN).
New Note (insert sub. Art. 31).

(Use 1st paragraph prop. 5 sub. Art. 32—by Hylander—beginning: "The "specific" epithet mentioned in Art. 31 . . ." etc.

Examples: (to be pared to essentials and corrected by Mr. STEARN). *Delete* HYLANDER'S "Note."

Article 32

Prop. 6—CAMP—Accepted *in toto*)

Add to it as "notes" the following:

"Note 1. "Hybrid subgenera" and "hybrid sections" may be named in the same way."

"Examples: *Iris* subg. × *Regeliocyclus*, including the hybrids between species belonging to subg. *Regelia* and to subg. *Oncocyclus*, respectively." (Have Mr. STEARN check example.)

"Note 2. The binary ("specific") epithet of an intergeneric hybrid must not be placed under the name of either of the parent genera."

(Mr. STEARN can furnish examples where this unfortunate practice has been used—if thought advisable to include in text.)

Article 33

(Prop. 4—CAMP—accepted with the following changes.)

1st line, 1st word—change "Terniary" to "Ternary."

3rd line, last word—change "polygeneric" to "multigeneric."

New Art. 33 bis—HYLANDER—to be considered in Appendix VII.

Rec. XX—to be deleted.

Article 34

(Prop. 5—CAMP—; accept 1st paragraph *only*—beginning):

"When the different hybrid forms of . . ." etc. (delete example and following note)

(add, as second paragraph, the following, modified from prop. 4—HELLYER):

"These forms are recognized as nothomorphs; when desirable they may be designated by an epithet preceded by the binary name of the group and the term nothomorph (*nothomorpha*, abbreviated as *nm.*), in the same way as subdivisions of species are classed under the binary name of the species.

Example: *Mentha* × *niliaca* *nm.* *Lamarckii*.

(Mr STEARN probably could furnish a better example.)

New Art. 34 bis—HYLANDER.

Not accepted.

New Arts. 34 ter, 34 quater, 34 quinquies—by Camp—rejected by Committee in favor of a separate Article—which was *accepted* by the Congress section as a *Recommendation*.

New Recommendation

(to follow Art. 34.)

Taxa which are apomicts may, if so desired, be designated in the following manner:

1) If they are considered as of specific rank, by the intercalation of the abbreviation "*ap.*" between the generic name and the epithet.

2) If they are considered as of infraspecific rank, by the intercalation of the abbreviation "*ap.*" between the category term and the infraspecific epithet.

In the case of an infraspecific category of a species which is wholly apomictic, the abbreviation "*ap.*" is placed solely between the generic name and the specific epithet.

Examples: (to be supplied by Mr. STEARN).

Taxa which are clones may, if so desired, be designated in the same way as for apomicts, except that the abbreviation "*cl.*" or the symbol CL is used in place of "*ap.*"

Examples: (to be supplied—*Hemerocallis fulva cl. Europa*).

New Paragraph—prop. Art. 34 bis—HYLANDER—not accepted.

§ 7. Names of plants in cultivation

Article 35

Plants brought into cultivation from the wild and which differ in no fundamental way from the parent stocks bear the same names as are applied to the same species and subdivisions of species in nature.

Plants arising in cultivation through hybridization, mutation, or other processes which tend to establish recognizable differences from the parent stocks receive epithets preferably in common language ("fancy" epithets) markedly different from the Latin epithets of species or varieties.

Detailed regulations for the nomenclature of plants in cultivation appear in Appendix VII.

*

New Art. 42 bis }
New Art. 42 ter } withdrawn by proposer.

Refer New Art. 42 quater to Comm. on Cult. Pl.

*

Insert *new-proposal*. Article 44 quater (to be actually located by the Editorial Committee).

For purposes of valid publication, names in Latin form given to hybrids are subject to the same rules as those of non-hybrid taxa of the corresponding rank.

Note: the parentage, so far as known, should be indicated.

Final Report: Committee on the Nomenclature of Cultivated Plants

It is to be recognized that those who name horticultural plants usually are dealing with three category levels—the generic, and what, on philosophical grounds, might be called the specific and infraspecific levels.

Generic names of plants originated in cultivation, whether referring to hybrid or non-hybrid taxa, are thought now to be adequately taken care of in the Rules. The formulation of specific and infraspecific epithets for plants originated in cultivation, when in Latin form also is adequately treated by the Rules through certain modifications accepted in current legislative decisions by this body.

There remains, however, a necessity for regulations for the forming of that large body of epithets on the specific and infraspecific levels, not in Latin form, and of especial pertinence to the nomenclature of cultivated plants. These regulations, if they are to appear with the Rules of Botanical Nomenclature, must be dealt with in a special Appendix which, as will be obvious, cannot be as yet voted on by this body but first must be referred to a parallel body of horticulturists.

It is therefore hoped that the authorities of this Botanical Congress will make overtures to

similar authorities of the International Horticultural Conference with a view toward arranging a joint meeting of the members of the Committee on the Nomenclature of Cultivated Plants of the International Botanical Congress with the members of the similar committee of the International Horticultural Conference so that a final draft of regulations, acceptable to both horticulturists and botanists, may be forthcoming.

To this end it is proposed that the present Committee on the Nomenclature of Cultivated Plants, as approved by this Congress, be given plenary powers to meet with a similar committee of the Horticultural Conference and complete the draft of such a set of regulations.

Pending such joint action it would seem unnecessary to present a full draft representing the current activities of this committee; it is perhaps sufficient to indicate that our committee has brought together the draft of a possible Appendix VII, primarily as a basis for discussion with the committee of the Horticultural Conference.

This draft has been a welding together of what, in our unanimous opinion, are the best elements of the various proposals brought forward for this Appendix and which already are on record. If we have made any major modifications these are in a direction seeking greater cohesion between Appendix VII and the current Rules of Botanical Nomenclature and also to accommodate recent advances in experimental horticulture.

Our guiding principle has been to disencumber botanical nomenclature, in so far as possible in the future, of unnecessary epithets in Latin form by strongly advocating the use of vernacular epithets for infraspecific categories of cultivated plants. Among cultivated plants these quite often are ephemeral and soon pass from the literature. To assist in this disencumbering of botanical literature we also have advocated, for plants originated in cultivation, dropping the category of variety and substituting the category of horticultural variety or "cultivar." In fact, to emphasize that the

horticultural variety usually is a thing biologically quite apart from the botanical variety we have further advocated that these horticultural epithets ("fancy names") be appended directly to the botanical name and, in addition, be further signalized as being this type of epithet by inclusion in quotation marks.

The same principle has guided our proposals for the epithets of hybrid groups where there is great complexity and wherein the parental formulae become unduly cumbersome, as in the wellknown garden materials derived from *Lilium* (*L. dauricum* \times *L. maculatum*) \times *L. davidii* var. *wilmottiae*. These might be given a collective epithet in Latin form, if so desired—and under the new Art. 44 quater, requiring a diagnosis in Latin. It is our suggestion, instead, and so as not to encumber botanical literature, that precedent be followed and that such complexes be given special names in the vernacular and their hybrid nature clearly indicated—e.g. *Lilium* "Preston Hybrids."

We have also advocated, where such hybrid complexes are further selected for particular series of characters (in this example, primarily for erect vs. nodding flowers), that these be designated as "groups"—e.g. "Preston Hybrids"—"Stenographer Group" and "Fighter Group"—wherein Miss PRESTON named individual selections of one group for her stenographers and those of the other group for fighter aircraft.

In brief, it has been our aim in formulating a preliminary draft of Appendix VII to emphasize the great desirability for the producer of new horticultural materials to employ epithets in the vernacular (i. e. "fancy names") for individual plant selections, reserving epithets in Latin form for special cases. The publication of such epithets in the vernacular is entirely outside the Rules of Botanical Nomenclature; it is dealt with in detail in our proposed draft.

Lastly, in recognition of the great need for special categories in what might be called "precision nomenclature" desirable both for experimental horticulture and experimental botany we have made further suggestions.

Three of these categories, namely apomict, clone and nothomorph, now appear in the Rules, since they are widely used today in general botanical literature. Others, at present primarily

of pertinence to the nomenclature of plants originated in cultivation, appear only in our draft of Appendix VII.

SUPPLEMENT III

Paleobotanical Nomenclature as accepted by the Congress

Art. PB 1

Since the names of the species, and consequently of many of the higher (taxa) taxonomic groups of fossil plants are usually founded on specimens of detached organs and since the connection between these organs can only rarely be proved, *organ genera* (*organogenera*) and *form genera* (*formagenera*) are distinguished as taxa within which species may be recognised.

An *organ genus* is a genus whose diagnostic characters are derived from single organs of the same morphological category or from restricted groups of organs connected together.

A *form genus* is one that is maintained for classifying fossil specimens that lack diagnostic characteristics indicative of natural affinity but which for practical reasons need to be provided with binary names. Form genera are artificial in varying degree.

Notes. 1) Organ genera based on detached parts may be distinguished not only by morphological characters, but also by reason of different modes of preservation.

2) It is necessary to distinguish both *organ genera* and *form genera* since the former are held to indicate a certain degree of natural affinity, while the latter may—and in many instances are known to—include species belonging to different families or even groups of higher rank e.g. ferns and pteridosperms. But form genera have been recognized as pertaining to a special morphological category since 1828 (ADOLPHE BRONGNIART) since that time they have been constantly used in taxonomic and morphological literature and they are quite indispensable.

Art. PB 2

The general principles applicable to all plants and to the nomenclature of taxonomic groups according to their categories are to apply also to the names of species of fossil plants and to organ genera and form genera (see Recommendations 1–3) (vide I. R. Chapt. III).

Conditions and dates of valid publication of names

Art. PB 3

From Jan. 1st 1952 the name of a genus or of a group of higher rank is not considered as validly published unless it is accompanied by a description of the group or by reference to a previously and effectively published description of it.

Art. PB 4

The type of a *genus of fossil plants* is the first described species which shows such characters as are necessary for distinguishing the genus from other groups.

The type of a *species of fossil plants* is the first described and figured specimen showing such characters as are necessary for distinguishing the species from other species.

Art. PB 5

When diagnostic characters are altered or circumscription changed in groups of fossil plants, the type is determined by reference to the original specimen figured in validation of the name of the taxon. If more than one figure applied in validation of this name, the emending

author shall indicate from specimens originally figured the one he regards as constituting the type.

Art. PB 6

The name of a monotype genus of fossil plants published after Jan. 1st 1952 must be accompanied by a description of the genus indicating its difference from other genera.

Recommendations

Recommendation 1

In describing organ genera it should be clearly indicated for which kind of organ the genus is established.

It is desirable that the names should indicate the morphological category of the organ. (For leaves a combination with *phyllum*, for fructifications combinations with *carpus* or *theca* etc.)

Recommendation 2

The names of form genera should, as a rule be used only with their original meaning and subsequent alteration of the diagnostic characters of form genera is not desirable.

Recommendation 3

Form genera should not be used as types on which natural taxa of higher rank are established.

Note: While organ genera may be grouped in families bearing names taken from one of the genera and ending in *-aceae* form genera should not be placed in groups with names implying the status of natural taxa.

Recommendation 4

In describing organs of uncertain nature or affinities, a name suggesting definite relationship with a recent plant should be avoided.

Recommendation 5

In describing a new species it is desirable to mention which specimen is regarded as the type and to indicate in which museum or collection the type is to be found.

Recommendation 6

Paleobotanists should exercise great caution in applying to well preserved specimens names which have been originally attached to poorly preserved specimens or to specimens which have been inadequately described or figured.

Additions to Appendix III

Nomina generica conservanda: Paleobotany

Fam.	Nomina conservanda	Nomina rejicienda
Ordo. <i>Pteridospermales</i>	<i>Doleriotheca</i> Halle	<i>Discostachys</i> Grand'Eury
<i>Megalopteridaceae</i>	<i>Megalopteris</i> (Dawson) Andrews	<i>Cannophyllites</i> A. Brongn.
<i>Calamariaceae</i>	<i>Calamites</i> A. Brongn.	<i>Calamitis</i> Sternberg
Ordo. <i>Cordaitales</i>	<i>Cardiocarpus</i> A. Brongn.	<i>Cardiocarpus</i> Reinw.
Form Genus	<i>Glossopteris</i> A. Brongn.	<i>Glossopteris</i> Rafinesque
<i>Taxodiaceae</i>	<i>Metasequoia</i> Miki ex Hu & Cheng	<i>M. disticha</i> (Heer) Miki
	genotype: <i>M. glyptostrobooides</i> Hu & Cheng	(no name rejected)
	(Other proposals on p. 234, were withdrawn.)	

Appendix IV

Nomina Ambigua

Proposal 5, p. 235 is withdrawn.

SUPPLEMENT IV

Report of the Special Committee for Fungi as accepted by the Congress

Article 10

Prop. 1

They have voted to inform the Section that they regard either Art. 10 or Art. 10 Prop. 1 as a correct statement concerning mycological classification.

Article 11

Prop. 1 & 2

They are agreed that *formae speciales* should not be treated as varieties; in this they oppose the adoption of the last sentence of Art. 11 Prop. 2.

They have voted to recommend that "*forma biologica*" and succeeding words be deleted from Art. 11 Prop. 1 and the rest of Prop. 1 be adopted. In the event that students of other groups wish to retain "*forma biologica*" not only as a category but in a fixed place in the series of categories, they still wish to delete the words "*Forma specialis* (in parasitic species)." They desire to retain the latter category, as provided in Rec. I, but without a hierarchical position.

Recommendation I

They have voted to recommend the retention of Rec. I with the substitution of "taxa" for "forms" where "forms" first occurs in the Rec., and with two corrections in text: "specific" to replace "special" (the latter apparently being an error of printing or transcription), and the plural "*formae speciales*" to replace "*forma specialis*."

Article 3

Prop. 1

They have voted unanimously to recommend again the adoption of the following amendment to Art. 13 Prop. 1, which they have already recommended to the Section and which has not yet been acted on: "An exception is made for names of subdivisions of genera in FRIES's

Systema mycologicum, which are treated as validly published although he termed them "tribes" (tribus)."

The committee do not believe that the phanerogamists will wish to force upon the mycologists a new provision, however desirable to the former, which would seriously disturb the now legitimate nomenclature and typification used by the latter.

Recommendation VII

Prop. 1

They have voted to recommend that Rec. VII Prop. 1 be adopted only if amended by striking out "the valid" and all succeeding words and substituting the words "it may be desirable to accept the type of the pre-startingpoint author." The version printed on p. 30 of the Synopsis, being in the form of a rule, is not approved.

Article 20 (e), (f), (h)

They have voted unanimously to recommend the retention of Art. 20 (e), with the date fixed as Dec. 31, 1801 and of (h).

They have voted to urge the adoption in place of Art. 20 (f) of the following: "(f) Fungi caeteri, 1821 (FRIES, *Systema mycologicum* Vol. I). Vol. I of the *Systema* is treated as having appeared Jan. 1, 1821, and the *Elenchus fungorum* 1828 is considered to be a part of the *Systema*. Names of Fungi caeteri published in other works between the dates of the first and last parts of the *Systema* which are synonyms or homonyms of names of any of the Fungi caeteri included in the *Systema* do not affect the nomenclatorial status of names used by FRIES in this work."

They unanimously recommend the rejection of Art. 20, Prop. 6.

Article 39 bis

They have voted to recommend the rejection of the note in new Art. 39 bis. They believe that the matter should be dealt with in Art. 57, where it is now treated of in Prop. 1.

Article 57

They have voted to recommend the adoption of the following text in place of the present Art. 57:

"In *Ascomycetes* and *Basidiomycetes* with two or more states in the life cycle (except when they are lichen fungi), but not in *Phycomycetes*, the first valid name or epithet applied to the perfect state takes precedence. The perfect state is that which bears asci in the *Ascomycetes*, which consists of the spores giving rise to basidia in the *Uredinales* and of the chlamydospores in the *Ustilaginales*, or which bears basidia in the remaining *Basidiomycetes*. The type specimen of a state must bear that state. However, the provisions of this article shall not be construed as preventing the use of names of imperfect states in works referring to such states.

The author who first describes a perfect state may use the specific epithet of the corresponding imperfect state, but his binomial for the perfect state is to be attributed to him alone, and is not to be regarded as a transfer.

When not already available, binomials for imperfect states may be proposed at the time of publication of a perfect state or later, using either the specific epithet of the perfect state or any other epithet available.

Article 64

Prop. 2, 3, 5, 7

They have voted to recommend that Art. 64 Prop. 2 be adopted. It is to be noted that the vast majority of names which have been affected by this Rule are fungus names.¹

Article 64

Prop. 4 & 8

They unanimously recommend the adoption of the following sentence, formed from Props. 4 and 8: "For nomenclatural purposes names given to lichens shall be considered as applying to their fungal components, but shall be subject to the provisions of Art. 20 (d)." It is to be noted that the word "exclusively," a part of Prop. 7, is not a part of this sentence nor of its provisions.¹

Appendix III

They unanimously recommend the conservation of the following generic names (subject to withdrawal if their nomenclatorial status is changed by modifications in the Rules adopted at this Congress): *Aleurodiscus*, *Calvatia*, *Clavaria*, *Daldinia*, *Marasmius*, *Melanogaster*, *Panus* (vs. *Pleuropus*), *Pleurotus*, *Septobasidium*, *Stagonospora*, *Tomentella* (vs. *Caldesiella*), *Tubercularia*, and *Uromyces*.

The citations, types or lectotypes, and *nomina rejicienda* have already been discussed in print and will be supplied to the Editorial Committee.

¹ The Committee's recommendations regarding Art. 64 have already been adopted by the Section.

PALEOBOTANY, PB

President: H. HAMSHAW THOMAS

Vice-Presidents: H. N. ANDREWS, C. A. ARNOLD, P. CORSIN, T. M. HARRIS,
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SUZANNE LECLERCQ, F. STOCKMANS, J. WALTON

Recorder: R. FLORIN

Vice-Recorder: O. H. SELLING

SESSION 1

Jointly with Section MOR: July 12th, 1—4 p. m., Attendance: 90 members

Chairmen: H. HAMSHAW THOMAS and A. J. EAMES, *Recorders:* R. FLORIN and F. FAGERLIND

SUBJECT:

The Telome Theory, Particularly as Applied to the Pteridophytes and the Pteridosperms

H. HAMSHAW THOMAS (Cambridge)

Opening Remarks

Before beginning our programme this afternoon, I should like to say how pleased we palaeobotanists are to visit Stockholm and how much we appreciate the excellent arrangements that seem to have been made for our meetings. The great progress made in the study of fossil plants during the 50 past years is in large measure due to the ideas and example which have come from Sweden, especially from Professor A. G. NATHORST, his successor Professor T. G. HALLE and also from Professor R. FLORIN. Early in this century the work of many palaeobotanists was mainly carried on in museums and laboratories. The collection of fossil plants in the field was left to professional collectors and field geologists. In England, at least, I remember Dr. D. H. SCOTT saying that palaeobotanists had to wait for something new to turn up. But NATHORST went out to various parts of the world and collected for himself the

specimens he wished to study. He and HALLE came to England and showed us that it was possible to discover many new forms. I do not think that I should be speaking here today if I had not profited from this example, and started to dig into the rocks of the Yorkshire coast and search for new types.

Then in another direction NATHORST brought about a change in the attitude of botanists towards fossil plants preserved as compressions. By reviving and improving the older methods of making cuticular preparations, he showed that such specimens were really mummified plants and not mere inorganic films or marks on the rock. The possibility of studying some of the microscopic features of these forms not only improved their status as objects for study, but it indirectly led to Professor J. WALTON's discovery of the peel method of preparing thin sections of petrified material, which has helped us so much.

We remember too the discovery of pollen grains in peat by Professor G. LAGERHEIM, and

NATHORST's early description of spores from the Höör sandstone.

We therefore come to Stockholm like pilgrims to the shrine of some famous saint, and I feel sure that like the devout pilgrims we shall draw inspiration and encouragement for our work from our visit.

But while thinking, as I must do, of NATHORST and of the time when I came here 39 years ago to learn everything that I could from him, I must also recall the way in which death has thinned the ranks of palaeobotanists since we last held an international meeting at Amsterdam. Among those whose faces we miss today are ALBERT CHARLES SEWARD, Lady ISABEL BROWNE, BIRBAL SAHNI, PAUL BERTRAND, LOUIS LAURENT, EDWARD WILBER BERRY, MIHAIL DMITRIEVITZ ZALESKY, JULIUS PIA, KURT FRENTZEN and S. ŌISHI. Other palaeobotanists who have died are HELENA BANDULSKA, T. D. A. COCKERELL, R. GRAHAM, A. V. JARMOLENKO, N. JOHANSSON, J. LANGER, J. LILPOP, P. MARTY, L. MORELLET, O. POSTHUMUS, W. REICHARDT, H. RÜHLE von LILIENSTERN, J. SCHUSTER, K. K. SHAPARENKO, A. L. DU TOIT and J. TUZSON.

Let us hope that their places will be filled by an even greater number of young men and women, and that the progress of our science will be still more substantial in the years to come than in the past.

H. HAMSHAW THOMAS (Cambridge)

The Telome Theory and the New Morphology

In discussing the telome theory and its applications, I wish to direct your attention to some of the philosophical aspects of plant morphology, which have, I think, been too much neglected, at least in English-speaking countries.

The comparative study of plant form involves the establishment of some frame of reference within which any structure under examination may be placed in its appropriate position.

Classical morphology or typology takes as

its standard for comparison an ideal plant composed of three distinct portions, roots, stem and leaves. As Dr. AGNES ARBER has recently pointed out, GOETHE's "*Urpflanze*" is an intellectual concept from which the concepts of existing forms could be derived by mental processes. The relationships conceived between different forms are thus connections which exist only in men's minds and are subjective notions. Typology is, of course, a perfectly valid mode of investigation and it has produced valuable results, but it is not the only method.

We have good reason to believe that a connection exists between plant forms and structures which is quite independent of man and his thoughts. This has been described as belonging to the realm of *materialistic philosophy*. This view considers that the similarities and differences between organisms are due to descent from common ancestors and modification of form and structure in a series of descendants through long periods of time. By correlating all the known information relating to the life and the reproduction of plants, including the facts of plant physiology and ecology, genetics and ontogeny, as well as consideration of internal and external structure, we may form some idea as to when, how and why changes in form occur.

The overall study of the history of plant form shows clearly that certain changes in external form and internal structure have taken place during the last 300 or 400 million years. The general trend of these changes established by the methods of historical research provides a view, possibly provisional, but none the less real, of a succession of organisms growing ever more and more varied in form.

This succession provides a new frame of reference for plant structures. The materialistic outlook on plant form is the basis of what I call the new morphology. It is complimentary to the old morphology rather than antagonistic to it.

The relation of the old morphology to the new may be made clearer by an analogy to the

study of the city of Stockholm. Its plan and construction may be

a) compared with that of other cities by referring all of them to an idea of the form of an ideal city, or

b) studied with reference to its history and the way in which its different parts or features have developed from primitive settlements on the site.

Now it seems to me that the telome theory can be treated either as providing a new ideal of plant construction formed in men's minds, and so is a new development of idealistic and subjective morphology. Or it can be regarded as a summary or interpretation of historical evidence and can become the basis of the new morphology. I prefer to regard it in the second sense, because it does amount to a summary of the changes which our historical records lead us to believe took place in the latter half of the Palaeozoic period.

W. ZIMMERMANN (Tübingen)

Cytologische und anatomische Basis der Telomtheorie

1. Das Ziel der "Telomtheorie" als eines Gliedes der "Neuen Morphologie" ist: möglichst wirklichkeitsgetreu den phylogenetischen Weg zu schildern, auf dem die Pflanzen, insbesondere die Kormophyten, geworden sind.

2. Unsere erste Aufgabe besteht daher darin, sichere Ahnengestalten zu erkennen. Durch statistisch-phylogenetische Methoden lässt sich eine Ahnenreihe folgender Gestalten aufstellen: Einzeller-Typ → Fadentyp → Urtelomstand repräsentiert durch *Rhyniaceae* → *Hemikormophyta* (z. B. *Protopteridiales*) → *Kormophyta*. Diese Typen treten in den geologischen Zeiten nacheinander auf.

3. Auch die *Ontogenie* vieler Kormophyten rekapituliert diese Ahnenreihe.

4. Die Gestalt der *Urtelomstände* stellt gewissermassen einen Engpass dar, der von der Pflanze auf ihrem Weg einer Eroberung des Festlandes durchschritten worden ist.

5. Nach Lösung der ersten Aufgabe (Ahnen-

gestalten) ist die zweite Aufgabe (die Schilderung des *phylogenetischen Ablaufes* selbst) relativ leicht zu lösen. Wir können ja den phylogenetischen Wandel an den späteren Formen, bzw. am Unterschied gegenüber den Urformen, ablesen. Ich beschränke mich auf eine Besprechung der *Verzweigungsphylogenie*.

6. Die beiden Haupttypen der Auszweigung, Emergenz- und Telom- oder Auszweigung, zeigen die Beteiligung folgender Elementarprozesse: Zellverkettung, Zellachsendrehung und Polarität. Das (auf nach-ordovizische Gewächse beschränkte) Zusammenspiel dieser drei Elementarprozesse führt zu den verschiedenen Formen der Auszweigungen. Beispielsweise greift die polare Organisation in drei verschiedenen Formen ein:

a) durch Lokalisierung der Ausstülpungen an bestimmten Zellpolen;

b) die Beeinflussung der Zelldrehungen am Vegetationspunkt in einem (vom wachsenden Pol durch einen Hemmungsabstand rhythmisch gelenkten) Abstand. Hierdurch bilden die Auszweigungen ein bestimmtes Muster (bekannt bei den Blattstellungen, aber auch schon bei verzweigten Fadenalgen);

c) durch rhythmische Drehungen der Zellachsen am Vegetationspunkt, was zu einem 3-dimensionalen Wachstum des Vegetationspunktes führt.

7. Diese Achsendrehungen (Drehungen der cytoplasmatischen Zellachsen) lassen sich *experimentell* beeinflussen, z. B.

a) bei verzweigten Fadenalgen durch Ausschalten des wachsenden Poles;

b) bei Kormophyten (*Pulsatilla*) durch bestimmte Gene.

8. Telome sind Einheiten einschliesslich des zunächst protostelischen Achsenstranges. Daher kopiert die *anatomische Umbildung* weitgehend die äussere Umgestaltung.

9. Das wird deutlich bei den *Pteridophyten*, wo die karbonischen Formen durchweg noch primitive Stadien (z. B. häufige Dichotomien, regelmässig katadrome Übergipfelung, Telome meist wenig verwachsen, oder wenn verwachsen, meist mit freien Adern usw.) repräsentieren.

10. *Heutige* Pteridophylle sind meist erheblich komplizierter. Aber auch die komplizierten Kombinationen (z. B. hinsichtlich der Katadromie und Anadromie) sind für die einzelnen Taxa sehr charakteristisch. Dies wird von der Taxonomie noch viel zu wenig verwertet.

11. Dieselben Umbildungen wiederholen sich in den *Achsen*. Die Protoxylemauszweigungen z. B. der Wurzeln sind meist noch recht primitiv. In den Sprossachsen werden die Anastomosen ähnlich wie in den Blättern erst im späteren Oberkarbon häufiger.

12. Phylogenetische Verschiebungen solcher Auszweigungen zeigen, dass — entgegen dem alten Homologie-Begriff — die determinierenden Reize auf nicht mehr homotope Gewebepartien wandern können. (Beispiele: die *Sphenopsida* mit ihrer erst später auftretenden Blattalternation, aber auch jede Planation.)

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H. N. ANDREWS (St. Louis, Mo.)

The Telome Theory with Reference to the Early Ferns and Pteridosperms

It is my feeling that the telome concept presents a useful term that may be conveniently applied to certain of the more primitive vascular plants of the Devonian and Carboniferous. It is evident, however, that it has limitations and should not be used indiscriminately.

It is my intention to consider certain phases in the evolution of the megaphyllous leaf; and the progression from a plant with an undifferentiated "shoot" system such as *Rhynia* to one in which leaves, stems, and roots exist as distinct morphological and anatomical entities involves stages in which the conventional terminology does not suffice. The telome concept introduces a term that allows one to express more accurately the change that is taking place.

The most significant phases in the evolution of the megaphyll from a psilophyte ancestor seem to be:

1. differentiation of stem and leaf
2. flattening of the frond into two-dimensional form
3. lamination of terminal telomes
4. dominance of monopodial over dichotomous branching.

We may first consider a new *Botryopteris* from the Pennsylvanian of Illinois. The principal specimen on which the description is based consists of a stem with five fronds attached. The latter are closely aggregated (being about 6 mm apart), branch in two planes, and the terminal divisions apparently lack lamination. Of particular interest is the vascular system. Upon leaving the stem stele the leaf "trace" is a massive, tangentially elongated strand which trisects into a central W-shaped strand and two lateral which are terete. The latter in turn trisect at right angles to the first division. In this trisection the laterals also are stelar, the proximal one being nearly as large as the stem stele and strikingly similar to it. We have, therefore, a "frond" in which there is a considerable retention of stem anatomy as well as one that is primitive in its three-dimensional branching and lack of lamination.

Our knowledge of the evolution of a flattened leaf is still rather sketchy. Some evidence bearing on the transition is shown by *Diplopteridium teilianum* in which the frond is divided into a central fertile branch and two sterile laterals. The latter present rather primitive "pinnules" and the fertile portion branches at right angles to the plane in which they are flattened.

The frond of *Telangium affine* may next be cited as an example of one in which two-dimensional form seems to have become established yet in which dichotomous branching is retained as well as the telomic nature of the ultimate branchlets. Numerous other examples may be cited (such as *Pecopteridium defrancei* and *Lonchopteris bricei*) of generally more advanced fronds yet ones in which dichotomy is

still conspicuous in the major divisions of the frond.

The evolution of the pinnule may well have taken place by fusion of ultimate frond branchlets. As an example of this the series *Rhacopteris petiolata*—*R. geiki*—*R. transitionis*—*R. inaequilatera* may be cited as typical.

While the telome concept is useful in many cases it must be recognized that it has its limitations. W. ZIMMERMANN has, for example, pointed out the difficulty, if not impossibility, of recognizing a telomic unit in an angiosperm leaf. Many other examples may be cited, such as the *Dolerotheca* fructification or seeds in general, which may well have evolved by some way other than telomic fusion.

In the same way that GOETHE's classic treatise on metamorphosis incited botanists to interpret all spore bearing organs as "sporophylls" it would seem equally misleading to attempt a universal telomic interpretation of plant organs.

P. CORSIN (Lille)

Morphologie des Fougères et des Ptéridospermées houillères

Des progrès ont été réalisés durant ces dix dernières années dans la connaissance de la morphologie des Fougères et des Ptéridospermées houillères notamment par les travaux de l'École lilloise de Paléobotanique.

Pécoptridées. Il est acquis maintenant que le *Megaphyton* possède des frondes divisées, en deux pennes symétriques, par dichotomie égale du rachis principal (1). Le nouveau genre *Hagiophyton* a été créé (2) pour des troncs de *Pécoptridées* possédant deux rangées diamétralement opposées de cicatrices alternes fort éloignées les unes des autres, et portant des frondes simples.

Mariopteridées. Grâce aux travaux d'un élève du Laboratoire de Paléobotanique de Lille, Mademoiselle PAULE CORSIN, on connaît, désormais, avec certitude la tige des *Mariopteridées* (3). Les édifices quadripartites sont des frondes, les axes sinueux qui portent ces

éléments sont des tiges. Le cycle phyllotaxique de *Mariopteris* est de 2/5; il est, suivant les espèces, dextre ou sénestre. Par déduction, on peut dire que les axes sur lesquels sont fixés les éléments quadripartites des plantes connues jusqu'à présent sous le nom de *Diplotmema*, sont également des tiges. D'autre part le dénominateur *Diplotmema* STUR prêtant à équivoque puisqu'il groupe à la fois des plantes dont la fronde est simplement fourchue et d'autres où elle est divisée en quatre sections d'égale valeur, le terme *Tetramema* (= *Diplotmema* pars) fut créé pour ranger les plantes possédant des frondes quadripartites avec limbe réduit autour des nervures. Le nom générique de *Diplotmema* emend. PAULE CORSIN sera réservé aux *Sphenopteris* à frondes divisées, par dichotomie, en deux pennes égales (4).

Sphénoptridées. Un autre élève du Laboratoire de Paléobotanique, R. SCRIBAN, a découvert la tige de *Sphenopteris* (*Diplotmema*) *striata* GOTHAN. Cette tige possède des caractères spéciaux (5): outre les stries longitudinales et les «barres» transversales, courtes et épaisses, dues aux fibres de sclérenchyme de l'écorce externe, elle est munie de cinq rangées d'épines coïncidant avec les cinq files longitudinales de pétioles. Le cycle phyllotaxique de *Sphenopteris striata* est sénestre et de 2/5 (6). On connaît également les tiges de *Sphenopteris* (*Diplotmema*) *neuropteroides* BOULAY et de *S. (Diplotmema)* *nummularia* GUTBIER.

Ainsi, on connaît, jusqu'à présent, les tiges de beaucoup de plantes fossiles rentrant dans les groupes du *Diplotmema* *adiantoides*, *Larischii* et *Hoeninghausi*, désormais, on les connaît également dans celui du *D. striata*.

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J. M. SCHOPF (Columbus, Ohio)

Male Fructifications of Some Paleozoic

Pteridosperms

Two subtribes have been established within the *Medullosaceae* to include groups of plants identified by characteristics of their male fructifications (SCHOPF, 1948, p. 686-7; HALLE, 1933, p. 8). I now propose to unite these two subtribes in a tribe to be named *Dolerotheceae*, tribus nov.

The *Dolerotheceae* are distinguished by their tubular sporangia, probably in paired arrangement and fully immersed in sterile tissue; by the extraordinary and unique type of prepollen produced by these plants; and by the essentially endokinetic mode of sporangial dehiscence (cf. JEFFREY, 1917, p. 218) that is indicated with a greater or lesser degree of certainty for various members of the tribe. No evidence for an ectokinetic mechanism has been shown in any instance and unless some evidence of this nature is discovered, we may tentatively be justified in regarding all members of the tribe as relatively advanced in this important characteristic.

A brief synopsis of taxa included in the *Dolerotheceae* is as follows:

Tribus: *Dolerotheceae*, tribus nov.

Subtribus: *Dolerothecinae* SCHOPF, 1948.

Genus: *Dolerotheca* HALLE, 1933.

Type species: *D. fertilis* (RENAULT, 1896) HALLE, 1933.

Other species: *D. formosa* SCHOPF, 1948.

D. villosa SCHOPF, 1948.

D. reedana SCHOPF, 1948.

D. sclerotica BAXTER, 1949.

D. schopfii BAXTER, 1949.

D. pennsylvanicum (DAWSON ex WHITE, 1903), comb. nov.

D. (?) cebennensis (GRAND'EURY 1890), comb. nov.

Subtribus: *Whittleseyinae* HALLE, 1933 (pro parte).

Genus: *Whittleseyia* NEWBERRY, 1854.

Type species: *W. elegans* NEWBERRY, 1854.

Other species: *W. microphylla* LESQUEREUX, 1884, p. 843.

(?) *W. integrifolia* = *crassifolia* LESQUEREUX, 1880, p. 524.

W. undulata LESQUEREUX, 1880, p. 525.

W. brevifolia WHITE, 1901, p. 104.

W. dawsoniana WHITE, 1901, p. 105.

W. desiderata WHITE, 1901, p. 102.

Genus: *Goldenbergia* HALLE, 1933.

Type species: *G. glomerata* HALLE, 1933.

Genus: *Boulaya* CARPENTIER ex HALLE, 1933.

Type species: *B. fertilis* (KIDSTON) HALLE, 1933.

Genus: *Aulacotheca* HALLE, 1933.

Type species: *A. elongata* (KIDSTON) HALLE, 1933.

Other species: *A. hemingwayi* HALLE, 1933.

A. campbellii (WHITE, 1899) HALLE ex ARNOLD, 1949.

A. (?) idelbergeri HALLE, 1933.

Genus: *Codonothea* SELLARDS, 1903.

Type species: *C. caduca* SELLARDS, 1903.

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Discussion

T. G. HALLE: Thanks to Dr. SCHOFF's investigations of well preserved American material of *Dolerototheca*, that genus has become by far the best known of the various kinds of microsporangial organs that are generally attributed to pteridosperms of medullosean affinities. The proposal to remove *Dolerototheca* from the *Whittleseyinae* seems well founded. It is unfortunate that the most completely investigated species, *D. formosa* SCHOFF, cannot be regarded as the type of the genus instead of the incompletely known *D. fertilis* (RENAULT) HALLE. However, the two species are undoubtedly congeneric. One of the most interesting features of *D. formosa* is that the radiating rows of sporangia are arranged in pairs. On the other hand, the sporangia themselves, as shown by Dr. SCHOFF's own illustrations, are far from always paired, i.e., they are not always opposite in each double row. Their arrangement thus lends no support to Dr. SCHOFF's far-reaching and in my opinion far-fetched comparison with the supposedly opposite sporangia of *Whittleseyia elegans*, even if these were always arranged in pairs, which is not the case. This matter, and the question of the symmetry of the *Whittleseyinae*, cannot be profitably discussed without detailed reference to illustrations; but I hope to return to the subject in another connection. Observations on specimens in the Coseley nodules, however, prove that neither *Aulacotheca* nor *Boulaya* were flat and leaf-like. Nor can this, as shown by microtome sections, be the case with *Goldenbergia*. To his excellent description of the structure of *Dolerototheca* Dr. SCHOFF has added a phylogenetic interpretation. He believes that this extraordinarily large and complex body has been evolved by the septation of a single

sporangium (fertile telome) rather than by the aggregation of free sporangia. I cannot share this view. It is contrary to the accumulated mass of facts bearing on the early evolution of the *Pteropsida*, and is neither supported by direct structural evidence, nor by convincing comparisons with possibly ancestral types. *Heterotheca*, to which reference is made, is an obscure object, and should be entirely disregarded in this connection.

J. WALTON: *Whittleseyia* is probably a campanulate structure, judging from the specimen figured by BOULAY as *Cyclopteris*, and I find it difficult to accept Dr. SCHOFF's interpretation.

J. WALTON (Glasgow)

Pteridosperm Fructifications

There is circumstantial evidence to support the view that the advent of heterospory led to a greater degree of protection of the sporangia by aggregation and sometimes encupulation of the microsporangia and by integumentation and encupulation of the megasporangia. The form of the integuments and cupules of the Lower Carboniferous *Salpingostoma* and *Calathospermum* with well developed vascular systems and pedicel strands, which are not radial in construction, suggests that the integument and cupule are morphologically equivalent structures and are not of cyclic construction in the sense used by HALLE. They may have been evolved by an inrolling process from an association of telomes which had already acquired a foliar, dorsiventral arrangement. In an ovule, one of the telomes became fertile and surrounded by the others.

In *Calathospermum* the cupule closely resembles the integument of the ovule. The vascular supply in the cupule stalk is like that of a petiole and the stalk itself is not much less in diameter than the petioles of the fronds of various types associated with it. The *Calathospermum* cupule may represent a complete frond such as *Diplopteridium* or *Telangium bifidum*.

The central branching system of pedicels in

Calathospermum may correspond to the dichotomously branching part of a *Diplopteridium* frond and the cupule lobes to the sterile part. In *Calathospermum*, however, the lobes are also fertile and each bears an opposite pair of ovule pedicels at its base. If the central group aborted and the lobes bore several pairs of pedicels, a cupule closely similar to *Dolerotherca* would be produced. If only one such lobe remained fertile, a cupule closely similar to that of *Caytonia* with its double row of ovules would be produced. The integuments in some angiosperm orders, which for other reasons are regarded as showing primitive features, have vascular bundles and it is difficult to doubt that the most likely forerunners of angiosperm carpels and integuments are to be found in Palaeozoic pteridosperms.

Discussion

J. M. SCHOFF: Professor WALTON's suggestion regarding *Dolerotherca* might be plausible if considered alone and apart from the Whittleseyian allies. The difficulty I have in accepting his suggestion arises from my belief that the *Whittleseyinae* and *Dolerothercinae* were closely allied and should be related in one tribe under the *Medullosaceae*. All that is known of the assemblage will have to be reconciled, rather than just the features of *Dolerotherca* alone.

Y. OGURA (Tokyo)

A New Pteridosperm and the Morphology of the Female Cone of Gymnosperms

Studying a seed-bearing fern-like fossil plant from the Permian at Penhsihu coal-field, Manchuria, I came to the conclusion that it is a new and good example of the pteridosperms. It was named *Pecopteris samaropsis* (1948), because a seed of the *Samaropsis* type is attached by means of a long stalk to the pinna-axis of a frond of *Pecopteris* type. Although in most

cases of the examples formerly illustrated as pteridosperms, the mode of attachment of the seeds to the frond is rather obscure, in the present specimen the organic connection of the two organs is very clearly shown. This suggests that a part of the frond becomes fertile and is transformed into an ovule. It should be remembered that in *Ginkgo biloba*, seeds are borne (abnormally) on the margin of the leaf, just as in several pteridosperms. The normal seed-bearing organ of this species resembles such an abnormal seed-bearing leaf in that it has a long stalk; but the stalks are not homologous, since four veins are found in the former and two veins in the latter. The stalk of this normal organ is situated in the axil of the scaly or normal leaf on the short shoot, and should be a branch on which a reduced leaf-bearing ovule is situated. The appearance of an abnormal seed-bearing leaf may be interpreted as an atavistic phenomenon, showing the first step of the seed-formation, and through the reduction of the lamina and petiole a new stalk should be formed, to which the extremely reduced leaf with ovules will be attached. The principle of this hypothesis is similar to that of STRASBURGER, FUJII or WETTSTEIN, but the mode of explanation is different.

This principle may be applied to the ovule- or seed-bearing organ of the conifers, in which the ovules are attached to the "seminiferous scale". This scale corresponds to the stalk in *Ginkgo*, being situated in the axil of the bract, which has a leafy character. However, the scale and bract are in most cases fused together, so that they cannot be distinguished as two organs. The ovule is attached to the scale, but theoretically on the extremely reduced leaf, which is no longer visible. This principle is like that of STRASBURGER or of VAN TIEGHEM, but the mode of explanation is different.

In the absence of the author an abstract of this paper was read by H. HAMSHAW THOMAS.

SESSION 2

July 14th, 9 a. m. — noon, Attendance: 50 members

Chairmen: O. A. HØEG and SUZANNE LECLERCQ

SUBJECT:

Various Papers

SUZANNE LECLERCQ (Liège)

*A Zygopterid from Upper Devonian Rocks*¹

In a quarry situated about 45 kilometers west of Liège, plant remains have been discovered in Upper Devonian rocks. Nearly all belong to the same plant, a fern, attributed to the genus *Rhacophyton* CRÉPIN. The plant here described is a new species and is named *R. zygopteroides*.

Most of the specimens represent fragmentary fronds, sterile and fertile; however, some of them have retained unexpected connection with their stem and main rachises; moreover, some of them are impregnated with iron mineral substance which has preserved their structure.

Consequently it has been possible to attempt a reconstruction of the external habit of the plant and to establish its relation with the *Zygopterideae*, a well represented group in the Carboniferous coal-balls. On the other hand, the anatomical study has strengthened the affinity with the *Zygopterideae*. The rachises have shown a *Clepsydropsis*-like petiolar strand which bears two rows of pinnae on the sterile frond and four rows on the fertile frond. The petiole trace has been followed in the stem and as a separate trace in the sterile and fertile fronds. The primary pinna trace and the pinule bundle are also known.

Finally, the results of the morphological investigations demonstrate such strong relations between the two genera *Rhacophyton* and *Cephalopteris*, both of Upper Devonian age, that it is proposed to fuse them into *Rhacophyton*, which is the oldest generic name.

¹ Preliminary note.

Discussion

R. KRÄUSEL: Professor LECLERCQ's material is much better preserved than that described by me and Professor H. WEYLAND from Western Virginia in 1942. Nevertheless we were able to show that *Rhacophyton* and *Dimeripteris* belong to the same genus and that *Cephalopteris* should be connected with this. We compared *Rhacophyton* with *Aneurophyton* of the Middle Devonian, and I think that *Rhacophyton* is a form connecting this primitive group with some of the *Primofilices* of Lower Carboniferous age. Professor LECLERCQ's investigation is a highly valuable contribution to our knowledge of Devonian plants.

C. A. ARNOLD (Ann Arbor, Mich.)

The Spores of Archaeopteris, with Remarks on the Affinities of the Genus

Archaeopteris latifolia, described by me from the Upper Devonian of Pennsylvania, is a heterosporous plant with distinct microspores and megaspores. The former are about 30 microns in diameter, and are borne in large numbers in slender sporangia that measure about 0.3 by 2.0 mm. The megaspores are about 300 microns in diameter, and are in sporangia measuring about 0.5 by 2.0 mm. The micro- and megasporangia can be distinguished from each other by their shape. Both spore types have thin smooth walls and simple triradial clefts.

Although this is the only species of *Archaeopteris* in which heterospory has been demon-

strated, it is suspected in *A. hibernica* and one or two others. The spore condition also shows that *A. latifolia* is not a seed plant, although the possibility that others might have borne seeds must be admitted. However, no positive evidence that any of the archaeopterids bore seeds has ever been produced. It is reasonable to assume that all species having typical archaeopterid fructifications reproduced by spores rather than by seeds. The genus is therefore to be regarded as a natural one. Carboniferous plants that have been assigned to *Archaeopteris* are incorrectly named as the genus is, as far as we know, restricted to the Devonian.

The *Archaeopteris* sporangium is borne in the simple terminal position, reminiscent of the *Psilophytales*. Each sporangium with its stalk may be interpreted as a telome, and a sporangial cluster is a telome cluster. The telome cluster represents the primitive condition, and the vegetative pinnule has developed by webbing of the sporangial stalks and loss of the sporangia. The vegetative pinnule is therefore homologous with a sporangial cluster, and is a syntelome. According to this interpretation, the vegetative pinnule has been derived from reproductive structures, a method of origin just the reverse of that postulated by the classical theory of the homology between leaf and fertile parts.

Some general resemblances between the foliage and spores of *Archaeopteris* and certain members of the *Noeggerathiales* are noted.

Discussion

T. G. HALLE: Dr. ARNOLD's account of the fertile pinnules of *Archaeopteris latifolia* is of great general interest. M. HIRMER has spoken of the sporangia of *Archaeopteris* as attached to the surface of the expanded pinnules, a statement which I have once, in passing, declared myself unable to accept as generally applicable to this genus. Dr. ARNOLD has now made it perfectly clear that the sporangia are terminal in position. They themselves seem to correspond to the ultimate sterile segments: to

represent fertile telomes homologous to the sterile telomes still recognizable in species with deeply dissected pinnules. Dr. ARNOLD's paper is in fact an important contribution to the discussion of the telome theory. The discovery of the heterospory in *Archaeopteris* reminds me, by the way, of the discussion at the Cambridge Congress (1930), when D. H. SCOTT and others remarked that the absence of reliable records of heterospory in Paleozoic ferns is an important negative factor to be considered in connection with the origin of the pteridosperms. This question now appears in a new light. Finally, the comparison made between *Archaeopteris* and the *Noeggerathiales* leads me to mention that in the megasporangia of *Noeggerathiostrubus bohemicus* I have found the spores to number 16. This observation, which I propose to publish shortly, agrees with Dr. ARNOLD's account of conditions in *Archaeopteris*. On the other hand, there seems to be no close relationship between the fertile leaves of *Archaeopteris* and the reproductive organs of *Noeggerathia*, which I still regard as representing cones (strobili). With this reservation touching a matter only in passing alluded to in the paper, I am in perfect agreement with Dr. ARNOLD's views.

C. A. ARNOLD: The number of megaspores in *Archaeopteris latifolia* and in *Discinites delectus* is 16 (or nearly so) in both plants. The dehiscence mechanism and cell structure of the sporangia was not observable in the material under consideration.

R. KRÄUSEL: Professor ARNOLD mentioned the close relationship between *Archaeopteris latifolia* and *A. hibernica*. Their sterile fronds are in fact indistinguishable. Professor H. WEYLAND and I were able to show in 1942 that *A. hibernica*, just as *A. latifolia*, has two different types of sporangia, and subsequently we also found the spores to differ in size. Unfortunately our slides were lost during the war. I entirely agree with Professor ARNOLD that *Archaeopteris* is a natural group, and that it does not include any seed plant.

J. WALTON: Has Professor ARNOLD found

any evidence of an annulus on the sporangia of *Archaeopteris latifolia*?

C. A. ARNOLD replied in the negative.

O. A. HØEG: *Svalbardia polymorpha* (HØEG 1942) from the uppermost Middle Devonian (lowermost Upper Devonian?) of Spitsbergen has sporangiferous shoots most strikingly resembling the fertile pinnae of *Archaeopteris latifolia*, but it is homosporous. Professor ARNOLD mentioned in his paper that this species evidently was the oldest heterosporous plant known. However, the fructifications found together with *Enigmophyton superbum* (HØEG 1942) in Spitsbergen, which probably belonged to that plant, were heterosporous, and they are older (occurring in the same strata as *Svalbardia*); but *Enigmophyton* almost certainly belonged to another phylum than *Archaeopteris*.

J. M. SCHOPF: I should like to inquire whether any analogy is possible between the exannulate sporangia of *Archaeopteris* and those of the calamites; and whether any dehiscence mechanism may have been uniformly, even though imperfectly, developed in the epidermal layer of sporangia?

C. A. ARNOLD: Some of the older figures of *Archaeopteris* sporangia show a longitudinal line supposed to be the dehiscence line, but no dehiscence mechanism was observed in the material I have reported upon. However, I am not prepared to deny the existence of such.

P. GUTHÖRL: Im Jahre 1940 haben M. HERMER und ich auf Grund meiner neuen Funde im Saarkarbon Untersuchungen durchgeführt, und es wurde die neue Unterfamilie *Noeggerathiinae* (*Filicales*) aufgestellt. In dieser wurden die Formen *Noeggerathia*, *Palaeopteridium* mit *Discinites* und *Saaropteris* mit *Saarodiscites* einbezogen. Ausschlaggebend hierfür waren die Fruktifikations-Organe. Wenn Herr ARNOLD seine fruktifizierende *Archaeopteris* mit *Discinites* vergleicht, so ist es ratsam, auch die übrigen Arten des Formenkreises *Noeggerathiinae* zum Vergleich heranzuziehen. Offenbar sind die fruktifizierenden Organe der hierher gehörenden Arten mit denen von *Archaeopteris* sehr verschieden in ihrem äusseren Aufbau.

N. W. RADFORTH: Did Professor ARNOLD discover any signs of spore development suggested by presence of immature and mature examples? Frequently spores in compact masses show a thin-walled non-ornamented condition, whereas spores loosely associated or isolated show a thick-walled condition and signs of ornamentation. Evidence of this sort is revealed in certain Carboniferous ferns.

C. A. ARNOLD: The spores of *Archaeopteris* appear to be consistently thin-walled and unornamented, whether isolated or in compact masses. No developmental stages or aborted spores, such as occur in *Calamostachys* or *Discinites*, were observed.

P. CORSIN (Lille)

La répartition stratigraphique des Pécopitéridées dans les Bassins houillers français

Les *Pecopteris* assez rares au début du Namuro-Westphalien du Nord de la France deviennent réellement abondants dès le Westphalien D et très abondants à partir du Stéphanien.

Dans cette revue de l'extension verticale des Pécopitéridées, je me bornerai, faute de place, à citer seulement les principaux *Pecopteris*.

Le Namurien est bien caractérisé par le *P. aspera*. Dans le Nord de la France, cette espèce est surtout abondante dans l'Assise de Flines (Namurien B). Toutefois on la trouve, à l'état sporadique, dans la base du faisceau d'Olympe (Assise de Vicoigne = Westphalien A) sensiblement jusqu'au niveau marin de Laure. En Vendée on la rencontre dans le Namurien inférieur.

Le *Pecopteris Volkmanni* SAUVEUR caractérisé par son maximum d'abondance l'Assise d'Anzin du Nord de la France (Westphalien B), mais il débute dans le sommet du Westphalien A (Assise de Vicoigne) et persiste dans le faisceau de Six-Sillons (base de l'Assise de Bruay = Westphalien C). Cette espèce a été retrouvée dans le Westphalien B de la Sarre (faisc. de Rothell).

L'extension verticale de *P. pennaeformis* BRGT est considérable puisqu'elle s'étend du Westphalien A (Vicoigne) jusqu'au Westphalien

C (Assise de Bruay et de Sulzbach). Toutefois on ne l'a jamais trouvé dans l'Assise de la Houve (Westphalien D).

Pecopteris Miltoni ARTIS (= *P. abbreviata*) est surtout fréquent dans les Assises d'Anzin et de Bruay (Nord de la France) ainsi que dans les Charbons gras (Westphalien B et C) de la Sarre. Cependant on a signalé cette espèce très haut dans le Westphalien D et jusque dans le Stéphanien. Je crois qu'il s'agit, alors, de *P. oreinervosa* nov. sp. (Flambants inf.) et de *P. opulenta* nov. sp. (Flambants sup.) qui ont été confondus avec *P. Miltoni*.

C'est à la base de la zone de Forbach de la Sarre que débute le *P. saraefolia-Röhli* qui persiste dans toute l'épaisseur de l'Assise de la Houve. Il est accompagné de *P. villosa* BRGT, *P. crenulata* BRGT, *P. longifolia* BRGT et de *P. punctata* nov. sp. qui ont sensiblement la même extension verticale. Dans les Flambants supérieurs apparaissent les *Pecopteris polita* nov. sp. et *P. victorae* qui montent dans le Stéphanien inférieur. La partie supérieure de l'Assise de la Houve est encore caractérisée par la présence des *Pecopteris saraepontana* STUR, *P. longiphylla* nov. sp., *P. micro-Miltoni* nov. sp., *P. Folschwillerensis* nov. sp. etc.

On note au sommet du Westphalien D (veine Heinrich de Puttlingen ou veine Aspen-Théodore) l'apparition d'espèces caractéristiques du Stéphanien: *P. lamurensis* HERR, *P. polymorpha* BRGT, *P. unita* BRGT, et des *Pecopteris cyathéoides* (*P. cyathea*, *P. arborescens*, *P. lepidorachis*, *P. hemithelioides* et principalement *P. pectinata* P. B.).

Les *P. lamurensis* et *P. arborescens* sont très fréquents dans le Stéphanien A (Rive-de-Gier). Ils disparaissent à la base de l'Assise de St-Etienne (Stéphanien B).

Les *Pecopteris cyathéoides* (sauf *P. arborescens*), les *P. unita* et *P. feminaeformis* ont leur apogée dans le Stéphanien moyen (St-Etienne). Enfin on trouve fréquemment dans le Stéphanien supérieur (= C) les *Pecopteris Momyi*, *P. Launayi*, *P. Wongi*, *P. Daubreei* et *P. densifolia*, cette dernière espèce apparaissant toutefois dès le sommet de l'Assise de la Houve.

Discussion

P. GUTHÖRL: Herr Kollege CORSIN hat sich die grosse und schwierige Aufgabe gestellt, die Pecopteriden des saar-lothringischen Karbons systematisch zu bearbeiten. Die vorbildlichen Arbeiten des Liller Instituts sind bestens bekannt, so dass man der Neuerscheinung mit Interesse entgegen sehen kann. Es sei jedoch darauf aufmerksam gemacht, hinsichtlich der Neugründung von Arten sehr, sehr vorsichtig zu sein, damit später die eine oder andere nicht wieder eingezogen werden muss. Es gibt eine grössere Anzahl von Pecopteriden im saar-lothringischen Karbon, wie ich es bei meinen karbonstratigraphischen Arbeiten in diesem Gebiet immer wieder feststellte, die zum Teil leitenden Charakter haben aber in nomenklatorischer Hinsicht noch im Rückstand, bzw. revisionsbedürftig sind. Es wird mit die Aufgabe von Herrn CORSIN sein, diese Fragen zu lösen.

W. J. JONGMANS: Il est extrêmement important que M. CORSIN publie un ouvrage tellement volumineux sur les Pécoptéridées. D'après sa conférence, il a créé un nombre d'espèces nouvelles. Je voudrais savoir si le nombre de ces espèces n'en devient pas trop grand et s'il ne s'agit pas plutôt d'une description d'individus bien conservés montrant un ensemble de détails que l'on ne peut pas découvrir sur des échantillons moins bien conservés. Dans beaucoup de cas, il est presque impossible de distinguer ces espèces, surtout lorsque, en les créant, on se laisse guider par des différences stratigraphiques plus ou moins grandes.

P. CORSIN: La description des Pécoptéridées du Westphalien et du Stéphanien de la Sarre comprend, il est vrai, un certain nombre d'espèces nouvelles. Parmi celles-ci, il y a des espèces figurées d'une façon trop rudimentaire par des auteurs anciens et que j'ai rebaptisées. D'autres sont réellement nouvelles; on pourra les distinguer par la forme et la grandeur des pinnules, par leur pilosité, par leurs caractères nervuraires, parfois même par leurs fructifications. S'il est difficile aujourd'hui de distinguer

les différentes espèces de *Pecopteris*, c'est qu'on n'en possède pas de bonnes figurations ou bien des figures trop petites. Je souhaite et j'espère qu'un ouvrage donnant d'abondantes images des divers *Pecopteris* servira à leur reconnaissance, et que leur détermination deviendra, grâce à lui, relativement aisée.

L. EMBERGER (Montpellier)

Les Préphanérogames

En 1942, l'auteur a distingué un embranchement nouveau, les Préphanérogames, groupant les Ptéridospermées et les Cordaïtes, jadis considérés comme Gymnospermes. Plus tard, à la suite des recherches ou observations de M. FAVRE-DUCHARTRE, M. CHADEFAUD, G. MANGENOT, P. MARTENS, il y a inclus les *Cycadales* et les *Ginkgoales*.

Les caractères qui justifient la séparation des Préphanérogames des Phanérogames sont les suivants:

1. absence de graine; dissémination d'ovules; alternance de génération du type ptéridophytique
2. structure de l'ovule (tégument complexe, vascularisation, etc.)
3. structure du pollen (Cordaïtes, *Ginkgoales*, *Cycadales*)
4. mégaspores fortement cutinisées
5. gamètes mobiles
6. diécie
7. le type foliaire, mégaphylle
8. fréquence du métaxylème centripète
9. traces foliaires habituellement doubles
10. présence d'un appareil sécréteur
11. stomates haplochéiles
12. déhiscence des anthères par exothécium (sauf *Ginkgo*).

Les Préphanérogames sont intermédiaires entre les Ptéridophytes et les Phanérogames.

Sont des caractères ptéridophytiques: Le corps végétatif souvent filicoïde (Ptéridospermées), la dichotomie relativement fréquente, le type d'alternance de génération, les mégaspores fortement cutinisées, parfois même encore libres, la déhiscence des microsporanges, les

gamètes ciliés, le prothalle bourré de réserves avant la fécondation; des caractères anatomiques, tels que la fréquence des structures archaïques, la structure primaire, etc.

Sont des caractères de Phanérogames: L'ovule, l'eustélie relativement fréquente, l'anatomie secondaire, l'endothécium de *Ginkgo*, etc.

Les *Cycadales* sont en rapports phylogénétiques avec les Ptéridospermées et les *Ginkgoales* avec les Cordaïtes.

Chacune des deux branches des Préphanérogames, par le relai de Gymnospermes (Bennettitiniées, Conifères), aurait donné naissance à des Angiospermes.

Discussion

H. N. ANDREWS: I believe that there may be some significance in Dr. EMBERGER's comparison of the sporocarp of *Marsilea* with the reproductive organs of the pteridosperms. There seem to be other features in the *Hydropteridineae* that are worthy of consideration; for example, the similarity in structure between the microsporocarp of *Salvinia* and the fructifications of the *Potonia* and *Doleriotheca* type. These comparisons may be very far-fetched but I feel that the "water-ferns" have certainly been neglected in our thoughts concerning seed-plant origin.

H. HAMSHAW THOMAS: It seems important in discussing classifications of widely different types of plants to distinguish between characters which may indicate common ancestry, and those which occur in diverse plants that are in the same grade of evolution. Some of the plants mentioned by Professor EMBERGER probably arose from very different ancestors at a remote period, but in the course of more or less parallel development they reached, at the same or at different times, very comparable forms and structures. Great caution must be exercised in the interpretation of the facts which have just been brought to our notice.

P. MARTENS: L'exposé de M. EMBERGER montre qu'il y a, de fait—et quoiqu'on puisse discuter la valeur de certaines d'entre elles—

des oppositions assez profondes entre les Gymnospermes inférieurs (Préphanérogames) et supérieurs (Spermatophytes vrais). Mais ce partage en deux groupes pose aussitôt la question de savoir si la vieille coupure entre Pteridophytes d'une part et Phanérogames classiques (incl. Préphanérogames), d'autre part, est encore valide. Le critère "fleur" (R. WETTSTEIN et al.) est pleinement illusoire, faute d'une définition satisfaisante, le critère "siphonogamie" est à rejeter, car il est en défaut pour plusieurs groupes, et le critère graine vient d'être écarté. Or il existe un critère valable, un caractère fondamental et exclusif pour toutes les phanérogames "classiques", et je crois qu'il n'y en a aucun autre! C'est la soudure originelle de la mégaspore au mégasporange, phénomène dont j'ai tenté de montrer la nature cytologique (Bull. Acad. Roy. Belg. 1947) et qui interdit congénitalement la dissémination de la spore. Pour le botaniste traditionnel, ce caractère permet de définir la graine. Au "préphanérogamiste", il permettra de définir l'ovule.

N. W. RADFORTH: There is, it appears, plenty of evidence suggesting that the phanerogams are strongly inclined to homospority, if spores are measured prior to prothallial development, an aspect that is important under this topic and one which relates for instance to Professor ANDREWS' suggestion concerning the importance of *Salvinia*.

J. WALTON: There is no satisfactory evidence of the production of free megaspores (embryo sacs) in *Schuetzia*. Absence of embryos in pteridosperm seeds (?) is probably due to the small chance of preservation under the circumstances favourable to petrification in the mass of vegetable debris forming the coal balls.

J. M. SCHOFF: Although *Lepidocarpon* and certain other groups show clear evidences of "phanerogamic" characters having been derived from a "cryptogamic" ancestry, we should not forget that both phanerogams and cryptogams are intensely heterogeneous groups, no longer spoken of in any sense representing natural classification.

P. DANGEARD: Je suis d'accord avec les

remarques de P. MARTENS au sujet de la distinction essentielle entre Cryptogames et Phanérogames. Les ovules de *Ginkgo* sont pollinisés de bonne heure tandis que la fécondation est retardée jusqu'au complet développement de l'ovule qui est devenu une graine renfermant un embryon au moment de sa chute de l'arbre, au moins sous le climat de Bordeaux.

P. W. THOMSON: Comment est la position systématique de *Voltziales*, surtout de *Lebachia* et *Ernestiodendron*? Le pollen est le même que chez les Cordaïtes et peut-être aussi les ovules.

L. EMBERGER: Les *Voltziales*, *Lebachia* et *Ernestiodendron* sont des Conifères authentiques, comme l'a définitivement démontré R. FLOREN. Les rapports phylogénétiques Cordaïtes → Conifères sont également très clairs et admis par les botanistes. Étant issus des Cordaïtes, il est naturel que les Conifères anciens cités aient retenu des caractères de la souche dont ils sont les descendants. Parmi ces caractères de Cordaïtes qui ont été transmis aux Conifères, il y a ceux de la conformité des grains de pollen et des traits de l'ovule. Même dans certaines formes actuelles survivent encore des vestiges de l'ancienne ascendance (exemple: ovule de *Tetraclinis articulata*, qui a des restes de sclerotesta). La position systématique des *Voltziales*, *Lebachia* et *Ernestiodendron*, me paraît donc très claire: elles font partie des Conifères, qui sont des descendants des Cordaïtes.

G. MANGENOT: Un caractère distinctif très net sur lequel on n'a pas suffisamment insisté sépare les Préphanérogames des Phanérogames: la zoïdogamie est la règle chez les premières, la siphonogamie chez les secondes.

R. POTONIÉ: Trotz aller Schwierigkeiten sind da Ideen, die verfolgt werden sollten.

K. JACOB (Calcutta)

The Stele in Tinpaharia, a New Genus of Petrified Mesozoic Ferns from the Rajmahal Hills, Bihar, India

The fern remains described in this paper were collected at Tinpahar, a newly discovered

fossiliferous locality in the Rajmahal Hills, Bihar, India.

The collection chiefly consists of the stems, rachises and roots of a fern, all found in organic continuity. Closely associated with these plant remains there occur the sterile and fertile leaf fragments of only one other fern, namely the well-known Jurassic species, *Coniopteris hymenophylloides* BRONGN. Although proof of organic continuity is lacking in this case, the circumstantial evidence is strongly in favour of the stems, petioles and roots being the petrified vegetative parts of *C. hymenophylloides*. As proof is not available, the petrified vegetative parts are described as a new genus *Tinpaharia* after the locality Tinpahar. The species has been named *Tinpaharia sinuosa* JACOB.

The stems, which are long and slender, may sometimes be twisted and bent, but are frequently straight, lying close together in a block. The weathered surface of the stem shows spirally disposed C-shaped leaf scars, arranged in a 5/13 order. Scars of numerous adventitious roots are also present scattered on the surface.

The branching of the stem is described in detail. The two arms of a branched axis may be either equal or unequal.

The most characteristic feature of the stem as seen in transverse section is the stele. This is a fluted and discontinuous vascular ring with numerous prominent exarch protoxylem groups and with the margins of the meristeles more or less turned outwards at the leaf gaps.

The cortex is differentiated into a sclerenchymatous outer and a parenchymatous inner region. The stele is dictyostelic. Each protoxylem group has an enclosed island of parenchyma. The metaxylem is mixed with a few parenchymatous cells. Sieve tubes are recognizable only in the outer phloem and here they are prominently developed. The pith is differentiated into an outer parenchymatous and an inner sclerenchymatous region.

The departure of the leaf-trace is described in detail. At least five groups of exarch protoxylem are present in the earliest stage. The sinuous xylem band of the leaf-trace is broken

in the middle, although the covering tissues, with the probable exception of the phloem, are continuous on both sides. Higher up in the free petiole the xylem again becomes continuous.

The rachis possesses a festooned xylem band with as many as twenty endarch protoxylem groups. The sclerenchymatous outer sheath of the rachis is generally well preserved, and in a cross-section it is seen projecting as a column from the adaxial side into the concavity of the petiolar bundle. The phloem and pericycle are generally not preserved.

Root-traces are seen arising both from the stem stele and from the leaf-trace. The stele has two exarch protoxylems with two prominent metaxylem elements placed in the centre, side by side, transversely to the two poles. The phloem is distinguished with difficulty. The other tissues are not clearly demarcated.

The associated sterile fronds show alternate, more or less cuneate pinnules of the sphenopterid type. Each pinnule has generally about fourteen veins in the broadest part. Like the petiole, the pinna rachis has an adaxial groove and contains an apparently sinuous xylem band.

A fragment of a fertile frond referred to *Coniopteris hymenophylloides* is also seen in association with the stems and petioles. It shows a few narrow, alternate, fertile pinnules, each terminating in one or more indusiate sori. A single sterile pinnule of the sphenopterid type is also seen attached to the rachis of the fertile frond.

The relationship of the sterile and fertile fronds with each other and with the rachis of *Tinpaharia* is fully discussed, and the conclusion is drawn that they probably belong together.

It is tentatively suggested that *Tinpaharia* was a fern possessing a long and slender, repeatedly branched rhizome which was probably ascending in its proximal parts and more or less erect distally.

Tinpaharia shows affinities both with the *Polypodiaceae* and with the *Dicksoniaceae*. Without further evidence it is not possible to refer the fern definitely to any known family.

But on the whole the evidence seems to favour a reference to the *Dicksonieae*. It is an interesting fact that the vegetative anatomy of *Tinpaharia* tends to confirm a reference of *Coniopteris hymenophylloides* to the *Dicksonieae* which was already suggested on independent grounds. While there is thus fairly good evidence that *C. hymenophylloides* was the foliage of *Tinpaharia*

sinuosa, absolute proof is still lacking; hence it seems advisable to refer the stems to a new genus for the present.

In the absence of the author of this paper the Chairman pointed out that an abstract had been distributed to the members of the section, and was also available for others interested.

SESSION 3

July 14th, 2—4.30 p. m., Attendance: 42 members

Chairmen: T. M. HARRIS and R. KRÄUSEL

SUBJECT:

Various Papers (continued)

C. A. ARNOLD (Ann Arbor, Mich.).

Silicified Mesozoic and Tertiary Plants of Western North America

The Mesozoic and Tertiary rocks of western North America are a vast repository of silicified vegetation that presents almost unlimited opportunities for research. These opportunities have been widely neglected for the following reasons: (1) the enormous area and few trained investigators, (2) difficulty in preparing the material for study, and (3) a prevailing notion that the effort expended would not be compensated for by the results obtained. The truth of the last can be effectively challenged.

Species preserved in greatest numbers are dicotyledons. These are followed in decreasing numbers by conifers, monocotyledons (especially palms), cycadeoids, and ferns. Only the cycadeoids have been comprehensively studied. The other groups have received only sporadic attention from paleobotanists. Recent investigations have revealed a wholly unsuspected wealth of fern material. An example is *Tempskya* with five species and more to be described, from fifteen or more localities. In the Clarno formation (Eocene) in Oregon, the massive tuff layers between rhyolite and basalt sheets contain cherty members evidently representing

silicified peat beds. These contain, along with other plants, species of *Osmundites* and the rhizomes of aquatic ferns of undetermined generic assignments. The situation seems to parallel somewhat that of the Deccan Traps in which important discoveries have been announced by the late Professor B. SAHNI and his colleagues. In the Oligocene and Miocene, particularly in areas covered by lava and ash, trunks of dicotyledons and conifers may often be observed standing where they grew, a classical example being the exposed stumps of Amethyst Mountain in Yellowstone National Park. Members of the *Taxodiaceae* are widely distributed and frequent, and specimens as much as, or exceeding, 5 m in diameter are recorded at several places. The silicified remains, if more thoroughly studied, would constitute a valuable supplement to the fossil record as revealed by leaf impressions.

K. A. CHOWDHURY (Dehra Dun)

Structure of Cell Wall in Ancient and Fossil Woods

A dozen dicotyledonous woods, about 2 000 years old and buried under ground, were examined. I also had occasion to examine more than three dozen fossil woods of Middle Tertiary

age. Microscopic examination shows that with age the wood fibres shrink and collapse, often forming into an irregular mass. The deterioration of fibre wall seems to begin from the inner side. In some cases the secondary thickenings of the wall disappear altogether. As a result fibres in cross-section show very thin walls. On the other hand, the vertical wood parenchyma cells and the rays retain the shape and the size of their cell walls, in spite of the age.

The question that now arises is what may be the reason for this. It is not yet possible, I am afraid, to give a definite reason for this behaviour of dicotyledonous woods. We know that parenchymatous tissues in wood, *i.e.* the vertical parenchyma cells and the wood rays, have numerous pits on their walls. These pits allow liquids to pass from one parenchymatous cell to another, and may thus help in the easy interchange of chemicals. But on the walls of wood fibres pits are usually scanty. This difference in their anatomical structure may be responsible for the difference in their behaviour to ageing. But at the same time we must not lose sight of the fact that so far very few tests have been done on pure samples of parenchymatous and prosenchymatous tissues. Except for a paper by HARLOW and WISE we have no information on the subject. The reason is obvious. It is a difficult task to separate parenchyma tissues from prosenchyma tissues in a piece of wood. However, we may be able to get over this difficulty and collect information on this point. This may then throw further light on the difference that we now find between the two main tissues of a dicotyledonous wood.

Discussion

W. W. VAROSSIEAU: Although my paper on ancient buried wood (*cf.* below) is only dealing with coniferous species, a great number of dicotyledonous woods from Rotterdam pilings have been studied. *Alnus* and *Betula* species that have been buried for up to 600 years show, already after this short period, features quite similar to those demonstrated by Dr. CROW-

DHURY in dicotyledonous woods buried for about 2 000 years. In the Rotterdam material, too, a decrease in thickness of fibre tracheid cell-walls is noticeable, as well as a break-down of cell-walls of vessels.

W. W. VAROSSIEAU (Delft)

Ancient Buried and Decayed Wood, from a Biological, Chemical and Physico-Mechanical Point of View

Object. The object of this study was to compare changes occurring in wood deteriorated by other agents than fungi during prolonged periods below the ground-water level, with changes occurring in wood decayed by fungal attack under aerobic conditions.

Changes in structure as well as in chemical composition and physico-mechanical properties were observed. In both types of material the influence of time on the processes involved was examined, and the interrelationship of these processes was studied.

Materials. During the German invasion of Holland (1940) the central part of Rotterdam was bombed and completely destroyed. A study was made of wooden pilings recovered from the foundations of the ruined buildings. These pilings, consisting of spruce (*Picea Abies* KARST.), pine (*Pinus silvestris* L.) and fir (*Abies alba* MILL.) had been buried for periods varying from 30 to 600 years.

This material was supplemented by lignite from brown-coal and still older material, such as jet. Samples of the latter, estimated to be 150 million years old, were provided by Dr. HEMINGWAY, of Leeds.

The wood attacked by fungi comprised material decayed both under laboratory and natural conditions. Only "brown-rot" fungi were included in the investigation.

Methods. The anatomical study was carried out with the aid of ordinary microscopic technique, phase-contrast and ultraviolet microscopy.

The chemical composition of the pilings was determined both in total cross sections, and in

1 cm thick layers successively peeled from the outside. Methods applied were those of KÜRSCHNER for cellulose, of TOLLENS for pentosans, and of RICHTER for lignin. Extractives soluble in alcohol-benzol were determined.

As regards the physico-mechanical characteristics, the following tests were made: specific gravity (in successive layers), bending, JANKA hardness, compression (direction of grain), shearing (MONNIN) and impact (IZOD and AMSLER tests).

Results. When wood is buried in the soil under anaerobic conditions, decomposition of the cellulose starts at the surface. With the passage of time, however, this process begins to extend to the interior, in some parts of the wood more rapidly than in others. Anatomical observations showed that the ray-cells are involved first. Thereafter the fibre tracheids near the growth-ring boundary and adjacent to the rays undergo attack. A similar type of break-down was observed in the cell-walls of subfossil and fossil wood buried in the ground for much longer periods than the Rotterdam material. The similarity becomes striking when a comparison is made of the following features: granular appearance of the cell-walls, dark coloured contents of the ray-cells, and shearing failures.

Bacteria proved to be present in nearly all types of buried wood.

Some of the features described in this material are also characteristic of decayed wood of the "brown-rot type", such as initial deterioration of rays and decrease in thickness of secondary walls. Other characteristics are only typical of fungal attack in *e.g.* bore-holes, with or without hyphae being present. Bacteria proved to be absent in decayed wood.

Chemical analysis of layers from Rotterdam pilings show clearly that decomposition of cellulose starts from the outside and proceeds towards the interior with the passage of time. Literature data on layer analysis of older buried material reveal the same type of wood decomposition. The decrease in the amount of cellulose causes an apparent increase in the lignin

content. Pentosans disappear in the course of time, but relatively slowly as compared to cellulose. After 350 to 450 years only 5 to 7 % of cellulose is left in the outer 1 cm layers of pine and spruce pilings. BRYDE (Norwegian Pulp and Paper Institute) determined the molecular weight of this cellulose by a nitration method. The molecular weight obtained corresponds with a D. P. of 3,400 and 3,500 glucose units in the first and third 1 cm thick outer-layers of a spruce piling, buried for 450 years. These unexpected high values might indicate a topochemical reaction, caused by the action of microorganisms. Anatomical observation clearly shows that no submerged fungi could be responsible for the cellulose break-down. The deterioration therefore might be due to bacterial action. Another possibility might be that a cellulose lignin bond prevents the cellulose towards the middle lamella from being degraded in such a way that the D. P. is lowered gradually. More evidence is necessary to prove these assumptions.

The type of break-down is the same in all species of buried wood investigated. However, fir yields the highest resistance to deterioration.

The chemical decomposition of wood attacked by "brown-rot" fungi is to some extent similar to the process described for buried wood. The cellulose and pentosan content decrease, whereas lignin is not attacked as much in the beginning. A striking difference, however, is the speed of decomposition, the fungal decay being effected within some months, the other process taking hundreds or even thousands of years. Moreover, in wood attacked by fungi under aerobic conditions the D. P. of cellulose is lowered gradually.

The loss in cellulose content has an equal effect on the physico-mechanical properties of buried and decayed wood. The specific gravity decreases in both cases (in buried wood it may ultimately increase again due to absorption of inorganic materials).

Swelling and shrinkage properties increase as compared to normal wood, and a noticeable longitudinal shrinkage originates in both de-

cayed and buried wood. These factors give rise to the "cubic rot" appearance of dried-out decayed wood and wood recovered from the soil.

Of the mechanical characteristics shock resistance is diminished earlier than any other of the determined strength properties. Also this feature holds true for decayed as well as ancient buried wood.

Conclusions. The investigation leads to the following conclusions:

1. The characteristic changes in the structure, chemical composition and physico-mechanical properties of the wood from Rotterdam pilings are to be considered identical with the first of a series of changes which wood undergoes during conversion to coal or during petrification.

2. With one exception no signs of the action of submerged fungi were present in the material recovered from the soil (below ground-water level). The break-down of cellulose seems to be due to a topochemical reaction.

3. Changes occurring in the structure, chemical composition and physico-mechanical properties of wood decayed under aerobic conditions by "brown-rot" fungi show a marked similarity with those pertaining to wood which has been buried below the ground-water level for a prolonged period of time.

4. A common cause for all features described which would account for their interrelationship might be a hydrolysis of cellulose, preceding further decomposition. This hydrolysis might be effected more rapidly by enzymatic action of fungi under aerobic conditions than by other micro-organisms or by a purely chemical action under anaerobic conditions below the ground-water level.

Discussion

R. POTONIE: Die Zellulose des Holzes verwandelt sich nicht restlos in Wasser und CO_2 ; sie verwandelt sich zum Teil in zu den Humus-säuren zu stellende Substanz und beteiligt sich als solche am Aufbau der Kohlen.

W. MÜLLER-STOLL: Ob die Zellulose an der Bildung der Humusstoffe beteiligt ist oder ganz verschwindet, kann vorläufig kaum sicher entschieden werden. Bei der vergleichenden Analyse zersetzten und unzersetzten Holzes müsste eine neutrale Bezugsgrösse gefunden werden, etwa ein beigemischter Stoff, der sich nicht verändert, und als Basis zur Umrechnung der übrigen Werte dienen kann. Die bisherige Vorstellung über die Beteiligung der Zellulose an der Huminkörperbildung sollte man nicht aufgeben, bevor nicht zwingende experimentelle Beweise dagegenstehen. Es sei auf die Entstehung kohlgiger und torfiger Massen aus Laubblättern und Moosen hingewiesen, die nur wenig oder kein Lignin enthalten. Es ist denkbar, dass unter bestimmten Bedingungen der Zelluloseabbau so verläuft, dass nicht nur CO_2 und H_2O entstehen, wobei wahrscheinlich rein chemische Abbauvorgänge an die Stelle der wohl vorwiegend biochemischen Hydrolyse treten.

W. W. VAROSSIEAU: I would be very interested to know what evidence there is to prove Professor POTONIE's statement. From investigations of my own material it appears that cellulose only shares in the formation of coal in so far as it has no time to disappear completely by a break-down to substances which do not contribute to coal formation.

W. MÜLLER-STOLL (Potsdam) *Die Diagnostik fossiler Dicotylenhölzer in ihrem Verhältnis zur rezenten Holzanatomie*

Fossile Laubhölzer werden schon seit über hundert Jahren untersucht. Bei der anfangs noch geringen Kenntnis der systematischen Anatomie der rezenten Hölzer konnten zunächst nur wenig verlässliche Ergebnisse erzielt werden, besonders hinsichtlich der tropischen und subtropischen Typen. Erst mit der Entfaltung der modernen Holzanatomie, gekennzeichnet durch das Erscheinen der ersten Bände des bekannten Werkes von MOLL & JANSSENIUS über die Holzarten Javas, wurden auch für die Bearbeitung fossiler Laubhölzer neue Grundlagen gefunden. Dementsprechend sind viele

Angaben in der älteren Literatur unzureichend begründet und führten zu einer mehr oder minder skeptischen Beurteilung der Diagnostik fossiler Laubhölzer, die jedoch nicht am Platze ist, wenn die Methoden und Erfahrungen der modernen Holzanatomie in der Paläobotanik Berücksichtigung finden. So erwies sich z. B. die Lochsortierkartei von Princeps Risborough als ausgezeichnetes Hilfsmittel zur Feststellung der Ausgangspunkte für eine genauere Untersuchung von Laubholzfosซิลien. Die durch die Intern. Assoc. of Wood Anatomists angestrebte Vereinheitlichung der holzanatomischen Begriffe und Standardgrößen ist bei sinngemässer Anwendung auf die Holzfosซิลien von bedeutendem Wert. Die Erforschung der fossilen Laubhölzer kann nur in enger Anlehnung an die rezente Holzanatomie erfolgen, woraus sich verschiedene wichtige Folgerungen ergeben:

1. Die anatomischen Merkmale sind bei fossilen Laubhölzern hinsichtlich des taxonomischen Zeigerwertes im wesentlichen nach denselben Maßstäben zu bewerten, wie es die rezente Holzdiagnostik verlangt. Die Beschreibung von Holzresten, die durch ihre Erhaltung kein eindeutiges Bild ihrer für die Bestimmung wesentlichen Merkmale geben, ist wertlos. Bei manchen Holzfosซิลien kann die Zugehörigkeit auch deshalb nicht sicher beurteilt werden, weil die in Frage kommenden rezenten Vergleichsformen ebenfalls keine sichere Unterscheidung zulassen oder erst unvollständig bekannt sind.

2. Der Nachweis ausgestorbener Formen durch holzanatomische Untersuchung der Laubholzreste ist noch nicht möglich, da über die in der rezenten Laubgewächsflora vorkommenden Strukturen heute noch kein ausreichender Überblick besteht. Hierin liegt ein wichtiger Unterschied gegenüber den Gymnospermenhölzern, bei denen wir ausgestorbene Typen seit langem mit Sicherheit erkennen können.

3. Die übliche Methode, für fossile Laubhölzer Formgattungen zu bilden, ist nur im engen Anschluss an die rezente Holzanatomie sinnvoll. Die fossilen Formgattungen müssen sich an die Strukturtypen der heutigen Gehölz-

flora anschließen und können nur insoweit Gültigkeit haben, als den Strukturmerkmalen der heutigen Vertreter taxonomischer Wert zukommt. Nur anatomisch wohl charakterisierte und abgegrenzte Gruppen der heutigen Gewächse sind zur Begründung fossiler Formgattungen geeignet. Ihr Typus im nomenklatorischen Sinne ist durch die rezenten Vergleichsformen gewissermaßen a priori gegeben; hieraus erwachsen gewisse Schwierigkeiten für die nomenklatorische Behandlung der Holzfosซิลien, die einer Lösung bedürfen. Es wäre sinnlos eine im Anschluss an eine bestimmte rezente Gruppe gebildete Formgattung beizubehalten, wenn die vermutete Beziehung sich später als irrig erweist. Zu allgemein gefasste, nicht auf eine anatomisch wohl charakterisierte rezente Gruppe aufgebaute Formgattungen sind zu verwerfen. Manche der älteren Namen sind von dieser Art, z. B. *Caesalpinioxylon*, *Accioxylon* u. a., da innerhalb der hierunter fallenden rezenten Vergleichsformen bereits eine Fülle von Verschiedenheiten vorkommen. Eine Formgattung braucht nicht und kann sich nicht immer auf eine einzige rezente Gattung beziehen, die für die Namensgebung gewählt wurde; es können zugleich verwandte Formen desselben Bautyps hierunter vereinigt sein. Formgattungen können auch auf Familien aufgebaut werden, wenn innerhalb dieser die anatomische Struktur des Holzes sehr gleichartig ist. Gelingt der Nachweis, dass ein fossiles Holz mit Bestimmtheit auf eine Form der heutigen Flora und nur auf diese bezogen werden kann, so handelt es sich nicht mehr um eine blosse Formgattung, sondern eigentlich bereits um eine gute Gattung im Sinne der rezenten Taxonomie. Unbedingt zu verwerfen ist das mitunter gewählte Verfahren, schlecht erhaltene Reste bei ungenau abgegrenzten, möglichst weit gefassten Formengruppen unterzubringen.

Bei richtiger Handhabung vermag die Untersuchung fossiler Laubhölzer wertvolle Beiträge zur Systematik und Biogeographie der kano-phytischen Flora zu liefern; die anhand der Blattfosซิลien gewonnenen Ergebnisse können dadurch gesichert und ergänzt werden, vor

allem hinsichtlich der tropischen und subtropischen Typen des älteren Tertiärs. Für das Gebiet von Mitteleuropa sind in jüngerer Zeit hiermit bereits ermunternde Erfolge erzielt worden. Die in Angriff genommene Nachuntersuchung alter Originalstücke unter modernen Gesichtspunkten lässt noch manches Neue erwarten.

ELISE HOFMANN (Wien)

Phosphatisierte Hölzer aus Prambachkirchen in Oberösterreich

Westlich von Linz in Oberösterreich liegen bei Prambachkirchen die burdigalen Phosphoritsande, die Fundstelle der phosphatisierten Pflanzenreste, die knapp vor oder während der Phosphatabscheidung gegen das Ende des Oligozäns in den küstennahen Meeresschlamm eingebettet wurden und deren Alter daher als oligozän angesehen wird.

Von diesem phosphatisierten Material wurden zumeist Anschliffe, seltener Dünnschliffe, für die mikroskopische Untersuchung hergestellt. Ich erhielt aus Prambachkirchen 1100 fossile Hölzer, die meisten phosphatisiert, wenige darunter verkieselt. Die Holzreste gehören Coniferen und Angiospermen an.

Neben überaus zahlreichen Resten von *Taxodioxyton sequoianum* GOTHAN finden sich Reste von *Cedroxyton prambachense* n. sp., charakterisiert durch rein parenchymatische Markstrahlen mit abietinoider Tüpfelung und äußerst dicht gelagerten Doppeltüpfeln in den Sommerholztracheiden, ferner *Piceoxyton prambachense* n. sp. mit Spiralverdickungen in den Tracheiden des Früh- und Spätholzes und sehr breiten Jahresringen, schliesslich *Pinuxylon prambachense* n. sp., welches in den parenchymatischen Markstrahlen grosse Eiporen und auch abietinoide Tüpfelung aufweist. Ausserdem sind auch nicht mehr bestimmbare Arten von *Cupressinoxylon*, *Cedroxyton*, *Piceoxyton* und *Pinuxylon* in dem Fundmaterial vorhanden.

Von den zahlreichen Angiospermenhölzern seien nur die interessantesten Arten herausgegriffen, wie *Casuaroxylon prambachense* n. sp.

mit seinen übermässig breiten homogenen Markstrahlen und den auffallend kleinen Gefässen, weiters *Fagoxylon Kräuselii* n. sp., das häufigst vorkommende Prambachkirchner Angiospermenholz, im Bau unserer *Fagus silvatica* sehr ähnlich, ferner *Quercoxylon prambachense* n. sp., in seiner Histologie unserer *Quercus pedunculata* sehr nahe stehend, weiters *Juglandoxylon Schadleri* n. sp. mit kurzen, tangential gelagerten Gefässgruppen und homogenen Markstrahlen, ferner *Magnolioxylon michelioides* n. sp. mit heterogenen Markstrahlen, die um die Gefässe meist geschlängelt verlaufen, weiters *Guttiferoxylon garcinoides* n. sp. mit seinem charakteristischen wellig verlaufenden metatrachealen Parenchym und seinen Zwilling- und Drillingsgefässen, sowie das äusserst feine und nahe verwandte *Guttiferoxylon prambachense* n. sp., ferner das überaus feine *Cunonioxylon weinmannioides* n. sp. mit para- und metatrachealem Parenchym in einzelligen Reihen, ferner *Leguminoxylon Piptadeniae* n. sp., charakterisiert durch sehr dicht getüpfelte Gefässe und heterogene Markstrahlen, weiters *Sonneratioxylon prambachense* n. sp. mit fast gekammert erscheinenden Gefässen und homogenen Markstrahlen, ferner *Rhizophoroxylon blepharistemmaoides* n. sp., ein überaus feinporiges Holz mit aller kleinsten Gefässen und sehr feinen para- und metatrachealen Parenchymbinden, ferner *Ebenoxylon Knollii* n. sp. mit einreihigen Binden von para- und metatrachealem Parenchym und heterogenen Markstrahlen, ferner das mit Zuwachszonen und stellenweise „doppelten“ Jahresringen gekennzeichnete *Tectonoxylon prambachense* n. sp., dann *Frazinoxylon prambachense* n. sp., unserer *Frazinus excelsior* histologisch nahe verwandt, und schliesslich *Rubioxylon naucleoides* n. sp., ein sehr feines, dichtes Holz mit einzeln liegenden Gefässen und ausgesprochen heterogenen Markstrahlen.

Ausser diesen neuen Arten finden sich dann noch Vertreter von Gattungen, deren Art wegen des schlechten Erhaltungszustandes nicht bestimmt werden konnte, wie *Alnoxyton* sp., *Carpinoxylon* sp., *Platanoxylon* sp., *Tetrameristo-*

xylon sp., *Leguminoxylon* sp., *Dombeyoxylon* sp., *Aceroxylon* sp., und *Agaurioxylon* sp.

Von Monokotylenresten verweise ich noch auf die interessante und wohlerhaltene Art *Palmoxylon phoenicoides* n. sp., im Bau *Phoenix dactylifera* sehr nahe stehend.

Sehr bemerkenswert ist auch noch ein wohl-erhaltener Same von *Juglans prambachensis* n. sp.

Aus dem Vorkommen zahlreicher wärme-liebender Hölzer in den Phosphoriten von Pram-bachkirchen kann wohl der Schluss gezogen werden, dass im Oligozän dieses Gebietes sub-tropisches bis tropisches Klima geherrscht haben mag.

Discussion

R. KRÄUSEL: Nachdem uns Professor ARNOLD auf den Reichtum der Vereinigten Staaten an fossilen Hölzern hingewiesen hat, freue ich mich, dass auch anderwärts ihre Bearbeitung in Angriff genommen wird. Ich bin überzeugt, dass sie einen noch längst nicht ausgeschöpften Beitrag zur Kenntnis älterer, besonders aber der tertiären Floren liefern können. Professor MÜLLER-STOLL hat auf einige der bei ihrer Bearbeitung auftauchenden Schwierigkeiten hin-gewiesen und mit Recht betont, dass eine der Voraussetzungen die Kenntnis der Anatomie rezenter Hölzer ist. Wo nur mit Anschliffen gearbeitet werden kann, wie bei dem von Pro-fessorin E. HOFMANN untersuchten Material, ist besondere Vorsicht und Zurückhaltung am Platze. Wir dürfen nicht in den Fehler älterer Autoren zurückfallen, voreilig Beziehungen zu rezenten Gattungen usw. anzunehmen, die sich später als unhaltbar erweisen.

P. W. THOMSON: *Ebenoxylon* ist ein interes-santer Fund im Oligozän, da die mit den Ebenaceen nahe verwandten Sapotaceen auch in dieser Zeit im mitteleuropäischen Raum verbreitet waren, wie es die Funde von H. WEYLAND in Rott (Rheinland) und der Pollen in der rheini-schen Braunkohle beweisen. Die Ebenaceen sind pollenanalytisch schwerer zu fassen.

CHINNA JACOB and K. JACOB (Calcutta) *Cuticles from the Tertiary Lignite of Cuddalore, S. Arcot, India*

This paper deals with cuticles of a few very interesting and important types of angiospermous leaves so far unreported either from the Tertiaries of India or elsewhere.

One of these types of leaves shows multice-lular peltate hairs both on the upper and lower surfaces. There are large hairs with more or less definite arrangement and smaller hairs of varying sizes which surround these larger hairs. The hair base consists of very thick-walled short cells. In the case of the lower cuticle the stomata are found round these thick-walled cells in one or two rows according to the size of the hair.

Leaves of this type are found in two sizes. Those of the smaller variety do not show any trace of the midrib while the larger type of leaves have a definite midrib. As both types show the same kind of cuticular structure and peltate hairs they may belong to the same family or even to the same genus.

These leaves are provisionally placed in the family *Oleaceae*.

There are a few other types of cuticles be-longing to other families also showing interest-ing features in the nature of their stomata, hairs, papillae, etc.

None of these leaves can be identified until the cuticles of the living plants with which the fossils show similarity have been studied in detail.

Two distinct types of fungi belonging to the *Microthyriaceae* and the *Trochopeltaceae* re-spectively were found to occur on the surface of these leaves. These are also described in detail in the paper. Both families of fungi thrive at the present day, usually in a humid tropical climate. It is the first time that such fungi have been reported from the Tertiary beds of India, although they have been de-scribed from similar beds in Europe and Aus-tralia (cf. page 586).

It is tentatively suggested that the Cuddalore

lignite flora thrived in a humid tropical climate somewhat different from the existing conditions in that region.

The age of the lignite is probably Late Miocene or Early Pliocene.

In the absence of the authors of this paper the Chairman pointed out that an abstract had been distributed to the members of the section, and was also available for others interested.

N. W. RADFORTH (Hamilton, Ont.)

Palaeoecological Research in Northern Canada

The presence of large tracts of ill-drained organic (peaty) terrain in the Canadian North provides a significant problem for foundation engineering and for northern development in general. This troublesome form of terrain is difficult to interpret in fundamental terms. Furthermore, because it varies in consistency the primary difficulty of interpretation is accordingly enhanced by secondary ones. To modify or to utilize it intelligently would seem ultimately to depend on the discovery and classification of its characteristics. To approach the latter problem palaeoecological methods are now being applied. The immediate objective is to establish a broad system of classification to serve as a basis for terrain typing.

The centre for field operations is Churchill, Manitoba, situated at the mouth of the Churchill River on Hudson Bay. Choice of this as the main area for investigation is significant from several standpoints. It is designated as sub-arctic and is located in the northern tree-line zone. Tundroid and boreal forest conditions

are both reflected. The climate is such that permafrost is a prominent component of the organic medium all summer long in certain areas under investigation. Characterization of terrain conditions indirectly by reference to surface vegetation alone is shown by our records to be inadequate and misleading. Plant communities are not sharply enough delimited, and there is an apparent indifference on the part of many plants to exhibit a consistent habitat preference.

Pollen and spore microfossils have been disclosed in sufficient enough numbers to facilitate the making of adequate counts. Particular reference is made here to microfossil analyses for two terrain types selected from a treeless heath-tundra. Among the tree pollens the grains of *Picea mariana*, *Picea glauca*, *Pinus banksiana* and the *Betulaceae* predominate. Among the pollens and spores of herbaceous plants, those of the *Cyperaceae* and *Sphagnaceae* are most significant, a fact which is reflected in the spectra of the two pollen-spore diagrams shown. The tree pollens are useful in providing an index for the whole area in an empirical sense. The pollens and spores of *Cyperaceae* and *Sphagnaceae* in these two diagrams show relative frequencies markedly different for each sub-area. Thus, two different patterns of organization are represented, and the basis for classifying each peat area is provided. Gross peat samples from the two areas were physically different, but they could only be differentiated in terms of designations too broad to be reliable or useful. Confirmatory evidence is now being sought to ascertain whether the methods applied will give consistently favourable results. Complementary quantitative investigations on macrofossils are proving encouraging.

SESSION 4

Jointly with Section PHG: July 17th, 9.30 a. m.—12.30 p. m., Attendance: 95 members

Chairmen: F. STOCKMANS and L. EMBERGER, Recorders: R. FLORIN and G. E. DU RIETZ

SUBJECT:

Tertiary Floras and Problems of Regional Phytogeography

R. KRÄUSEL (Frankfurt am Main) *Pflanzenwanderungen im Tertiär*

Versuche, die während des Tertiärs stattgehabten floristischen Veränderungen zu erkennen, sind so alt wie die Tertiär-Paläobotanik selbst (UNGER, von ETTINGSHAUSEN), sie sind auch in neuerer Zeit gemacht worden, besonders für die arktotertiäre Flora oder Teilgebiete derselben. Es ist indessen zu fragen, ob sie bei dem derzeitigen Stand der Tertiär-Paläobotanik zu sicheren Ergebnissen führen können. Nur für kleinere Räume, und auch da nur bei aller vorsichtigster und kritischer Auswahl, wird es zunächst der Fall sein können. Beklagenswert ist, dass die Untersucher in Nordamerika und in Ostasien viel zu wenig Rücksicht auf die europäischen Floren nehmen. Unter neuen Namen tauchen so sehr oft alte, europäische Formen auf, wodurch ein Vergleich erheblich erschwert wird. Ein zwar enges, aber günstiges Untersuchungsgebiet ist der Raum um Frankfurt am Main. Hier gibt es eine Anzahl von Floren, deren Alter als gesichert angesehen werden kann, und die vom Eozän bis zum Ausgang des Pliozäns reichen. Sehr schön lässt sich hier der Florenwandel von einer rein tropischen bis zu einer von der heutigen kaum noch verschiedenen Flora verfolgen, ein Wandel, mit dem das Verschwinden zahlreicher Formen Hand in Hand geht. Erweitern wir das betrachtete Gebiet, so entstehen neue Schwierigkeiten, da es recht oft schwer ist, das genaue Alter bzw. die Gleichaltrigkeit festzustellen. Hinzu kommt die Unvollständigkeit des Materials. Wir müssen es auswerten, ganz gleich, ob es sich um Früchte und Samen, um Sporen oder Hölzer handelt. In jedem Falle darf aber Vorsicht und Selbstkritik beim Versuch der Bestimmung

nicht ausser acht gelassen werden, was namentlich im Hinblick auf die tertiären Laubhölzer nicht dringend genug betont werden kann. Die Behauptung, die in tertiären Schichten so häufig vorkommenden Blätter seien völlig oder fast völlig wertlos, muss als masslos übertrieben abgelehnt werden, denn viele Blattformen sind schon nach ihren morphologischen Merkmalen eindeutig „bestimmbar“. Noch mehr gilt das dort, wo die Blattsubstanz erhalten ist und anatomischer Prüfung unterzogen werden kann. Diese „Kutikularanalyse“ (vergl. K. JURASKY, R. FLORIN, W. N. EDWARDS u. a.) verspricht am ehesten Erfolge, wenn sie auf solche Blätter angewandt wird, deren Form und Nervatur gleichfalls bekannt sind. Von diesem Gedanken ausgehend, haben R. KRÄUSEL und H. WYLAND eine Reihe seit langem bekannter tertiärer Formen untersucht und konnten ihre systematische Stellung weiter klären. Bezüglich Einzelheiten sei auf die in der „Palaeontographica B“ erscheinende ausführliche Arbeit verwiesen. Wir gedenken sie fortzuführen. Wenn andere diesem Beispiel folgen, wenn ausserdem wirklich alle Reste beachtet werden, die uns das Tertiär in so reicher Fülle liefert, dann wird es möglich sein, die grossen floristischen Veränderungen dieser Zeit und die Wanderwege der einzelnen Florenbestandteile zu verfolgen, weit sicherer, als es heute schon der Fall sein könnte.

E. S. BARGHOORN (Cambridge, Mass.) *Changes in the Generic Composition of Tertiary Floras of North America and their Relation to the Determination of Age*

Morphological study in conjunction with stratigraphic correlation has demonstrated fundamental units of vegetational change through-

out the geologic record of plant life. The major sequences of fossil floras have resulted from organic evolution, but within restricted geographic as well as stratigraphic limits, these changes reflect also the migration of plant populations. In major sedimentary series, particularly of the Paleozoic and Early Mesozoic, the sequence of terrestrial floras can be translated into a chronological sequence, and general relationship established between age, area, and plant population. Cenozoic sedimentary series of limited lateral and vertical extent, however, present difficult problems in the application of orthodox stratigraphic methods for determining either age or relationship. Understanding of Cretaceous and Tertiary floras which are uniformly featured by the abundance of angiosperms requires paleoecological analysis and comparison with existing plant associations. The problem is complicated by three factors: 1) difficulties of accurate botanical identification, 2) relationship of plant associations to special ecological conditions, and 3) profound climatic change during Cenozoic time. Efforts to elucidate the major changes in Tertiary vegetation therefore require composite analyses with reference to ecologic units in the living flora. These analyses demonstrate a clear statistical relationship between age, climate and generic composition of major Tertiary floras of North America.

K. A. CHOWDHURY (Dehra Dun)

Tertiary Floras and Problems of Regional Phytogeography in Eastern India

The Tertiary flora of eastern India has not so far been studied in detail, although geological reports mention the occurrence of leaf impressions and fossil woods from many localities. Amongst the leaf impressions definitely identified are *Ficophyllum burmense* EDWARDS and *Dipterocarpophyllum gregoryi* EDWARDS. As regards fossil woods, the form genus *Glutoxylon* CHOWDHURY has been recorded from four localities, and *Dipterocarpozylon garoense* CHOWDHURY from two localities. *Cynometrozylon*

CHOWDHURY et GHOSH has been reported from one locality; likewise *Kayeoxylon* CHOWDHURY et TANDAN.

A comparison of the distribution of these trees between Middle Tertiary and the present time shows a considerable difference indicating a trend of migration towards south and east. But there are some genera which show little difference in their distribution. The other conclusions drawn are:

The Middle Tertiary flora of eastern India so far shows only a tropical range.

No clue is yet available regarding the migration of some temperate genera to the hills of the Indo-Malayan region.

Discussion

L. EMBERGER called attention to the comprehensive work of the late Professor B. SAHNI on Indian fossil floras.

P. W. THOMSON (Liblar b. Köln)

Die Sukzession der Moortypen und Pflanzenvereine im Hauptflöz der rheinischen Braunkohle

Das bis zu 100 m mächtige Hauptflöz der rheinischen Braunkohle ist an der Oligozän-Miozän-Wende entstanden (Chatt-Burdigal). Der Kohlenstoss zeigt mächtige „dunkle Bänke“, in denen schon makroskopisch eine Holzföhrung zu erkennen ist. Gelegentlich schliessen diese dunklen Bänke mit ausgesprochenen Stubbenhorizonten ab. Mehr oder weniger scharf abgesetzt liegen auf ihnen fast holzfreie Schichten, die sich meist durch eine hellere Färbung abheben, die sog. „hellen Schichten“. Diese hellen Schichten sind aus halbblimnischen Cyperaceenmooren vom Everglades-Typus Floridas entstanden. Der Pollenreichtum ist ein sehr grosser, über 10 000 in 50 Milligramm Trockensubstanz. Im unteren Teil herrschen hier Pollenformen wie *Quercoidites henrici* R. POT. und rhoide Pollenformen vor, ebenfalls *Pollenites liblarensis* P. TH. Im oberen Teil *Quercoidites microhenrici* R. POT. und *P. villensis* P. TH.

(castanopsioide Pollenformen — THIERGART). Geschichtete Harzeinschwemmungen und eingeschwemmte Hölzer sprechen für periodische Überflutungen, wie in den Everglades. Ein grosser Teil dieser Pollenformen dürfte von Wäldern herrühren, die ausserhalb des Moores standen und der Familie der Cupuliferen angehören.

Die schon erwähnten „dunklen Bänke“ zeigen eine völlig andere Pollenzusammensetzung. Mazeriertes Holz, Korkgewebe usw. bilden die Hauptmasse der Braunkohle. Sehr verbreitet sind myricoide und betuloid Pollenformen in Verbindung mit Tracheen mit Leitdurchbrechungen und typischen Myricaceenkutikeln. Der *Pinus*-Pollen kann in mehreren Formen eine grössere Rolle spielen. Im unteren Teil sind besonders Pollenformen der Taxodiaceen und Cupressaceen häufig, ferner nyssoid Pollenformen und kleine Dreieckpollenformen — cf. *Engelhardtia*. Von der Mitte des Hauptflözes an und im oberen Teil spielt der Pollen und das Holz von *Sciadopitys* eine Rolle. Palmenholz (*Palmoxylon bacillare* BRONG.) ist auch häufig. Viel seltener der dazugehörige Pollen vom *Sabal*-Typus. Auch sapotoide Pollenformen und solche wie *Pollenites rotundus* R. POT. und *P. vestibulum* R. POT. (nach THIERGART Symplocaceen [KIRCHHEIMER]) treten hier auf. Auch Pollenformen wie *P. (cingulum) brühlensis* P. TH.

(cf. *Cyrillaceae*) und *P. pseudocastanea* P. TH. sind hier häufig. Ebenso der Ericaceenpollen und gelegentlich *Sphagnum*-Sporen.

Von Farnen treten ausser den Polypodiaceen auch die Osmundaceen und die Schizaeaceengattung *Lygodium* auf. Wir können hier Taxodiaceen-*Nyssa*-Gesellschaften, sowie Myricaceen-Gesellschaften mit und ohne *Pinus* unterscheiden. Bei noch geringer werdender Absenkung treten trockenere Waldtypen auf, in denen bes. der sequoioide Pollen und das meist gut erhaltene cf. *Sequoia*-Holz (*Taxodioxyton gypsaecum* GÖPP.) vorhanden ist. Hier haben oft Brände stattgefunden, die Brandfusitlagen hinterlassen haben. Die Pollenmenge ist in den „dunklen Bänken“ 5–10 mal geringer als in den „hellen Schichten“. Grosse cf. *Sequoia*-Stubben sind nur in den basalen Teilen und Randlagen vorhanden.

In diesem Wechsel der Cyperaceenmoore und Bruchwaldmoore mit Trockenlagen spiegelt sich der Absenkungsrhythmus wieder, dem ein zweiter Wechsel in der Gesamtvegetation — basale Elemente — terminale Elemente — übergeordnet ist, der klimatisch bedingt sein kann.

Ein gleicher doppelter Rhythmus ist von H. PRUG im Alttertiär von Helmstedt festgestellt worden, und auch im Karbon des Ruhrgebietes haben K. VON KARASIN und G. KREMP ähnliches feststellen können.

SESSION 5

Jointly with Section MOR: July 18th, 9 a. m. — noon, Attendance: 50 members

Chairmen: C. A. ARNOLD and P. MAHESHWARI, Recorders: R. FLORIN and F. FAGERLIND

SUBJECT:

The Female Cones of the Conifers

R. FLORIN (Stockholm)

The Female Reproductive Organs of the Stachyosperms

Our knowledge of the female reproductive organs in this major division of the gymno-

sperms has increased considerably since the previous Botanical Congress. A brief account of the results of recent researches is given.

As regards the *Ginkgo*inae these concern the morphology of the primitive genus *Trichopitys* of Upper Palaeozoic age and the living *Ginkgo*.

In the female sex the *Ginkgoinae* have wholly fertile sporangial trusses (strobili or flowers) occurring singly on long or dwarf shoots. They differ in that respect from the cordaites and conifers, in which the corresponding sporangial trusses are, at least primarily, composed not only of fertile but also of vegetative telomes and aggregated into compound strobili (inflorescences). In the *Ginkgoinae* the ovules are placed terminally on lateral branches of the poorly defined axis of the flower.

In the Upper Palaeozoic *Cordaitinae* two types of female flowers occur, one primitive and one more advanced type, of which the latter is transitional to that of the oldest conifers.

The conifers have been subjected to extensive investigations, particularly with the aim of solving the old problem of the morphology and evolution of the female cones. The cones of Upper Palaeozoic and Mesozoic types have been examined and found to provide the main clue to the interpretation of the living types. The great diversity in the latter is chiefly due to the transformation and differentiation in various directions of a primitive axillary fertile dwarf shoot and its accompanying bract.

The comparative morphology of the female reproductive organs in fossil and recent genera, usually referred to the *Coniferae*, has shown that they should be classified into two different subdivisions of the stachyosperms, the true conifers on the one hand, and the *Taxinae* on the other. The conifers are characterized by generally cone-shaped inflorescences, and ovules borne terminally on extremely reduced megasporophylls, which themselves are lateral organs on a more or less rudimentary floral (strobilar) axis. As in the *Ginkgoinae* and *Cordaitinae*, the integument consists of branches of the megasporophyll. The taxads, on the other hand, have no inflorescences of the conifer type, and the ovule is terminal on the floral axis itself. In their case the integument appears to be formed by whorled branches, corresponding in position to the megasporophylls of the conifers and alternating with the preceding whorl of scales on the axis.

The opinion, first expressed by SAHNI, that in the stachyosperms "the ovules and seeds are borne either clearly upon an axis or upon a structure which is some modification of an axis" appears to be sound.

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Discussion

T. M. HARRIS: Is there yet any hint of connection between the *Taxaceae* and the *Coniferales*? Also, what is Professor FLORIN's view of the origin of the *Taxaceae*?

R. FLORIN: There is no hint of any connection between these groups. Taxinean forms have been found as far back as in the Upper Triassic formation. This group may consequently be as old as, or perhaps even older than, the true conifers. However, the various groups of stachyosperms appear to be of a common origin, probably in the Upper Devonian or Lower Carboniferous.

P. R. BELL: Has Professor FLORIN any view of the phylogeny of *Juniperus*? In *Juniperus communis* the free ovules alternate with the innermost whorl of scales. This would seem to indicate a very highly modified seed-scale complex.

R. FLORIN: The *Oxycedrus* section of *Juniperus* takes up an exceptional position, in that its three ovules alternate with the cone-scales, and do not seem to be part of any seed-scale complexes. Abnormal cones with two fertile whorls of cone-scales have been found, however, in which each axillary seed-scale complex of the lower whorl contains two ovules. In view of the position of the ovules in several junipers of the *Sabina* section, and seeing that paired ovules sometimes also occur in *Oxycedrus*, it may be assumed that their normal position in

the common juniper is due to the suppression of one ovule in each flower, and to subsequent tangential displacement of the remaining ovule. This interpretation appears to be confirmed by the fact that here as in other cases the cone-scale consists of a strongly modified axillary complex united with a bract.

J. T. BUCHHOLZ: As one who has been critical concerning the validity of the *Taxales* as a group distinct from the *Coniferales* I have been trying to justify or to find the basis of valid objections to this classification. The result has revealed the existence of an important difference that has not been emphasized. It may have been overlooked. I refer to the vascular bundles found in the ovule wall of all or nearly all *Taxales*. The *Coniferales* have no vascular bundles in the ovule. In *Acmopyle* and *Podocarpus* the bundles found there belong with the ovuliferous scale, the so-called epimatium.

A. J. EAMES: Is it not possible that in *Juniperus communis* the ovules do not stand in an anomalous position (representing a shifting in position) but rather, that the members of the next whorl of units are in greatly reduced condition, the fertile scale consisting of little more than a stalk, as in *Pherosphaera*?

C. A. ARNOLD: The series of fossil forms connecting the cordaitan inflorescence with the coniferous cone is one of the most satisfactory ever to be brought to light. We are so often forced to resort to blackboard diagrams in postulating phylogenies. It tends to reestablish our confidence in the theory of evolution.

W. ZIMMERMANN (Tübingen)

Die radiären Strukturen der Sporangienstände (Sporophylle) in den Blüten

1. Die verschiedenen Formen der Sporangien und des Generationswechsels sind bei den Kormophyten nach quantitativ-phylogenetischen Untersuchungen auch in phylogenetischem Sinne einander homolog.

2. Aus diesem Grunde schliessen wir, dass

auch ihre Träger (die Sporangienstände) phylogenetisch zusammenhängen.

3. Die flächigen Sporangienstände, die heute dominieren, sind nach quantitativ-phylogenetischen Ergebnissen von radiären abgeleitet. Der Anteil der radiär-symmetrischen Sporangienstände (♂ sind nicht berücksichtigt) sinkt von fast 80 % im Unterdevon bis auf 17 % in der heutigen Flora.

4. Das peltate Sporophyll, z. B. der *Sphenopsida*, hat sich durch wenige phylogenetische Elementarprozesse (Inkurvations und Verwachsung) aus dem radiären Urzustand herausentwickelt. Eine Änderung der Symmetrie ist dabei nicht erfolgt.

5. Die von R. FLORIN erkannte Phylogenie der Coniferen zeigt wie sich im Schuppenkomplex aus radiärsymmetrischen Gebilden flächige Schuppen entwickelt haben.

6. Bei der Zentralplazenta der Angiospermen, die auf relativ wenige Taxa beschränkt ist, handelt es sich um eine Rückkehr zum radiären Urzustand, auf einem Umweg über ein flächiges Sporophyllstadium.

7. Ontogenetische Entwicklungsvorgänge, z. B. die Karpell-Ontogenie bei monospermen *Anemoneae*, beweisen nicht, dass in der Phylogenie die Samenanlagen unabhängig von den Karpellanlagen entstanden sind. Wenn man die Ontogenie beispielsweise von *Pulsatilla* mit der hier anfangs blattachselständigen Anordnung der Samenanlagen für eine Rekapitulation der Phylogenie ansehen würde, müsste man für *Pulsatilla* eine Lycopsiden-artige Urform annehmen.

8. Zu typisch phyllospernen *Ranunculaceae* vermittelnde Formen (wie *Olematis*) machen es aber viel wahrscheinlicher, dass der monosperme Fruchtknoten der *Anemoneae* vom *Helleborus*-Typ durch Reduktion abgeleitet ist.

9. Sobald man anerkennt, dass auch die Phyllome radiäre Urgestaltformen haben, und dass deren Merkmale heute noch nachklingen können, entspricht die BRAUN-ČELAKOVSKÝ'schen Phyllotheorie des Fruchtknotens noch heute am besten dem phylogenetischen Ablauf.

Discussion

A. J. EAMES: On the basis of anatomical evidence, angiosperms cannot be divided into phyllosperms and stachyosperms. All angiosperms are phyllospermous. Free central and basal placentation is always derived, usually from axile, rarely from parietal placentation. The division of angiosperms into these two groups would separate them into two wholly unrelated groups (unrelated since the Lower Cretaceous according to the scheme proposed by Professor H. J. LAM). Families generally recognized from evidence of all kinds become unrelated, the *Scrophulariaceae* and the *Lentibulariaceae*, for example; closely related genera become unrelated, *Drosera* and *Dionaea*, for example. The species of many genera become unrelated. *Lychnis alpina* is phyllosporous; other species are stachyosporous.

W. ZIMMERMANN: Ich stimme mit Herrn EAMES überein, als auch ich die Zentralplazenta durch Wegfall von Scheidenwänden aus einer zentralwinkelständigen Plazentierung entstanden denke. Meine Ausführungen sollten belegen, dass infolge dieser Umbildung die Symmetrie des Sporangienstandes wieder zum radiären Urtyp zurückgekehrt ist.

F. FAGERLIND: It has never been proved that the angiosperm carpel is a metamorphosed leaf. The other day Professor BLAKESLEE read (before the Section for Morphology) a paper by Dr. SATINA and himself entitled "Periclinal chimaeras, a tool in determining the contribution of germ layers to floral organs in *Datura*." The *Datura* carpel was proved to contain derivatives also from deeper layers than those producing leaves, sepals, and petals. Another observation of the same kind was made earlier. RÖSLER stated in 1923 that the leaf of wheat is derived exclusively from the outermost layer of the apical meristem. ÅKERMAN's investigation of wheat chimaeras shows that the wheat carpel, on the other hand, is partly derived from deeper layers. The experience with *Datura* and *Triticum* thus suggests that the carpel is something other or something more than a

simple leaf. In a paper dealing with the strobilus in the genus *Gnetum*, I pointed out that the carpel might be homologous with the cone scale of a conifer, i.e. with the sterile bract and its reduced fertile axillary shoot. If that is so, then the bract and the axillary product must have fused together into a single unit, which we call a carpel. It is of interest to note that evolutionary transformations of a similar kind have actually occurred in the conifers.

SUZANNE LECLERCQ: La planche établie par le Professeur ZIMMERMANN pour représenter la phylogénie du sporophylle chez les *Lycopsida* reproduit quatre stades successifs: A, B, C, D, dérivant l'un de l'autre, la forme A étant la plus primitive. Or les formes les plus anciennes connues parmi les *Lycopsida* fossiles donnent le stade D, dès le Dévonien inférieur avec le genre *Drepanophycus* et aussi dans le Silurien avec le genre *Baragwanathia*: c'est à dire un seul sporange par bractée (stade D) et non pas deux sporanges distincts se fusionnant progressivement (stades: A, B, C).

W. ZIMMERMANN: Auf die Frage der Phylogenie der blattachselständigen Sporangienstellung bei den Lycopsiden bin ich absichtlich nicht eingegangen. Diese Frage ist zu kompliziert, um in einem kurzen Sammelreferat ausreichend behandelt zu werden. Nur soviel kurz: die blattachselständige Sporangienstellung hat sich offensichtlich bei den Lycopsiden im Zusammenhang mit der Mikrophylle entwickelt. Namentlich die Anatomie (Gabelstrukturen der Stele und der Leitbündel), aber auch die gelegentlichen Gabelungen und gruppenweisen Vereinigungen der Telome bei *Baragwanathia* und *Drepanophycus*, sprechen für die Gültigkeit der Telomtheorie auch auf diese Gestalten. Überdies sind nach freundlicher mündlicher Mitteilung von Herrn Kollegen OZENDA neuerdings auch aus dem Altpaläozoikum die von Prof. LECLERCQ vermissten Übergangsstadien gefunden worden. Aus diesen Gründen halte ich es für wahrscheinlich, dass auch bei den frühdevonischen bzw. silurischen Lycopsiden die blattachselständige Sporangienstellung ebenso wie die Mikrophylle durch Anwachsen

ganzer Telomstände entstanden ist. Diese Umbildung hat aber offensichtlich schon sehr früh (vielleicht auf einem Tangstadium) stattgefunden.

BRITTA LUNDBLAD: The *Lepidopteris Ottonis* fructification might possibly have been surrounded by at least a temporary covering (cupule), and the reconstruction in current use reproduced by Professor ZIMMERMANN might be subjected to future modification. This is indicated by the result of a recent study of an impression from Höör in Scania (cf. LUNDBLAD in Kungl. Svenska Vetenskapsakad. Handlingar Ser. 4, Vol. 1, No. 8, 1950). The evidence obtained can, however, not be regarded as conclusive; a different interpretation of the Höör fossil has in fact been suggested.

H. GAUSSEN (Toulouse)

L'évolution du cône chez les Conifères

On admet, dans cette interprétation, la conception d'évolution pseudocyclique: un caractère passe au cours de l'évolution du phylum par un type primitif, en général compliqué, qui regresse en se spécialisant vers un type évolué simple.

La surévolution retrouve, en général par soudure, une complication qui rappelle le type primitif. Ce type compliqué est, à titre de type primitif, le point de départ d'un nouveau cycle.

Les idées morphologiques admises dans cette interprétation sont:

A. Le genre *Pinus* comporte dans son appareil végétatif deux types de feuilles. Euphylls placées sur tous les rameaux et en général réduites à des écailles. Pseudophylles (= aiguilles) formées par la division en long d'un rameau appelé schizoblaste.

B. Les autres genres de Conifères (sauf *Sciadopitys*) ne comportent que des euphylls dans leur appareil végétatif mais les pseudophylles sont conservées dans l'appareil reproducteur.

Le cône femelle apparaît comme un axe portant des brachyblastes. Au Permien, chez *Lebachia*, ce brachyblaste porte des euphylls bien constituées et un ovule. Chez *Walchiostro-*

bus fasciculatus le brachyblaste a l'allure d'un schizoblaste à pseudophylles porte-ovules. Si elles se soudent par surévolution on obtient un cladode aplati: *Pseudovoltzia* et *Ullmannia* présenteraient le type surévolué qui serait à l'origine d'un nouveau cycle au secondaire. Il s'agit de filiation de structures et non de filiation réelle.

Au Trias on verrait réapparaître une sorte de foliarisation du brachyblaste-cladode avec les types *Voltziopsis*, *Glyptolepis*, *Voltzia*, du Trias, avec *Schizolepis*, *Swedenborgia*, du Lias, encore plus divisés. Une nouvelle soudure en écaïlle se ferait avec *Hirmeriella* qui annonce le type des Conifères.

Alors que HAGERUP voit dans l'écaïlle du cône une feuille du type écaïlle de bourgeon empêchant le développement du brachyblaste, j'ai proposé une interprétation comme cladode (C. R. Ac. Sc. Paris, t. 227, pp. 731-733, 1948). Les nombreuses nervures, la présence de poils identiques à ceux des rameaux sont des arguments solides pour étayer cette interprétation.

Le schizoblaste court comme cladode aurait une partie proximale ramuliforme et une partie distale en pseudophylles. Dans l'écaïlle du cône de Pin, seule la partie proximale est développée; chez *Swedenborgia*, les deux parties sont égales; dans l'appareil végétatif de Pin la partie distale est seule développée en forme de pseudophylles. Il y aurait un cyclisme entre le type cladode et le type pseudophylle mais ces organes auraient une valeur de rameau.

Discussion

T. M. HARRIS: Is there not a small stem apex or abortive bud between the leaves of the dwarf-shoot in the pines?

H. GAUSSEN: Le brachyblaste normalement n'a pas de bourgeon, mais si dans le voisinage on a supprimé le bourgeon d'auxiblaste, les hormones de formation de bourgeon se produisent dans les brachyblastes les plus voisins qui forment des bourgeons et se transforment plus ou moins en auxiblastes.

J. T. BUCHHOLZ: I wish to point out that while

the growing point is present between the needles of *Pinus*, and may be stimulated to full development (transforming the dwarf shoot into a long branch), there is no such apex in a certain form of *Pinus Krempfii* with very large flat leaves.

J. T. BUCHHOLZ (Urbana, Ill.)

The Cones of Certain Rare Conifers of the Southern Hemisphere

The materials described and illustrated include species of *Araucaria*, several *Agathis*, 2 species of *Libocedrus*, *Neocallitropsis*, *Callitris*, 2 species of *Acmopyle*, 5 species of *Dacrydium* and 10 species of *Podocarpus*, nearly all from New Caledonia. The last named genus is represented by 5 sections. This includes all genera found on this island with the exception of *Austrotaxus* which was not found in reproductive condition.

All these cones conform to a uniform pattern in the attachment and arrangement of the morphological members of bract and scale complex, whether there are hundreds of cone scales as in *Agathis* and *Araucaria* or only one or a few fertile scales as in *Podocarpus*.

Among 8 species of *Araucaria* of New Caledonia one finds that in all of them the ligule is so small and suppressed that it might be overlooked. This condition is also shared by the

Australian species *A. Cunninghamii* and *A. Klinkii* from New Guinea. In *Araucaria Bidwillii* from Australia and in *A. excelsa* from Norfolk Island, the apex of the ligular appendage is swollen and stands out as a conspicuous pad that may be recognized externally on the intact cone. In both *Araucaria* and *Agathis* the cones are biennial — that is they are pollinated in the year preceding their enlargement and the maturity of seeds.

In *Cupressaceae* the bracts and scale complex are usually fused, diverging only at the apex, with 2 or 1 winged seeds erect and related to the fertile scales in axillary positions.

In *Podocarpaceae*, the scale complex is represented by the so-called epimatium arising from the base of a bract, where there may be a slight amount of fusion. The attachment of scales—the bracts and fertile members—always include an epimatium which surrounds the ovule and seed, partially in *Dacrydium* and completely in *Podocarpus* and *Acmopyle*. Ovules are single per bract-scale complex, but many were found with several fertile scales per cone in 3 sections of the genus, also in *Acmopyle* and *Dacrydium*. Added fertile scales are inserted in spiral order. While the cones of *Dacrydium* all follow the same pattern, a condition found in the cone of *Dacrydium Guillauminii* is of special interest in having a very short cone axis bearing numerous sterile scales, with many below and some above the fertile ones.

SESSION 6

July 18th, 2—3.50 p.m., Attendance: 40 members

Chairman: H. N. ANDREWS

SUBJECT:

Morphology and Phylogeny of Mesozoic Gymnosperms

T. M. HARRIS (Reading)

Nilssonia and its Reproductive Organs

Nilssonia (Rhaetic to Cretaceous) is the commonest and most completely known of fossil

cycads. The organs so far claimed as recognized are: Leaf (form, anatomy of lamina, cuticle of many species); scale leaf (form and cuticle); male cone (*Androstrobus*) (form of whole cone, form of microsporophyll, some details of spo-

rangia, pollen); female cone (*Beania*) (form of whole cone, form and cuticles of sporophyll); seed (external and internal cuticles and some of its anatomy).

It is suggested that the loose construction of *Beania* (even when immature) indicates a pendulous amentum-like organ, and this implies a fairly tall stem, perhaps of tree-form.

The stem is unknown, but a possible stem has been found in Yorkshire bearing scars suitable for the leaves, cones and scale leaves. Its cuticle is also suitable but does not point exclusively to *Nilssonia*, and it is only at present claimed to be a possible stem.

The reproductive organs agree closely with those of the *Zamia* group of *Cycadales*, except in the loose construction of *Beania*. If the *Cycadales* evolved from pteridosperms with elaborately branched sporophylls, then a great part of cycad evolution (reduction of sporophyll) must have been completed by Rhaetic times.

In conclusion it is pointed out that the circumstantial evidence on which the various organs are attributed to one genus might be strengthened if search were made in other floras.

H. HAMSHAW THOMAS (Cambridge)

The Relationships between the Bennettitales and Cycadales

The vegetative structures of the *Bennettitales* and *Cycadales* are so similar that they have often been considered as related in spite of the great differences in the form of their reproductive organs. While it is possible that the similarities are due only to parallel evolution, it is also likely that the differences in the reproductive structures appear to be greater or less according to the morphological interpretation given to these structures. Evidence is accumulating which suggests that the early ovulate cones of the *Bennettitales* produced only lateral structures of one type, orthotropous ovules on short stalks, many of these ovules were abortive and evolved into the interseminal scales of the

later species. A reexamination of the structure of the Triassic *Bennetticarpus* (*Williamsonia*) *Wettsteini* (KRASSE) gives considerable support to this view. The ovulate cones of the cycads are generally regarded as a group of megasporophylls, greatly reduced in the genus *Zamia*. But in spite of Prof. R. FLORIN's investigation of the form *Palaeocycas integra*, it should not be assumed that *Cycas revoluta* represents the most primitive form in the group. *Zamia* might well be the most primitive of the modern forms, a view supported by the Jurassic *Beania gracilis*. If these suggestions are correct, both the cycads and the *Bennettitales* may have been derived from some pteridosperm which, like the *Corytospermaceae*, had fertile axes bearing lateral sporangiophores, sometimes simple with terminal ovules and sometimes bifurcating with two ovules. The pollen bearing structures may have originated from structures of the *Crossotheca* type.

Discussion

R. KRÄUSEL: Dr. THOMAS sieht im *Zamia*-Megasporophyll die primitive Form gegenüber demjenigen von *Cycas*. In diesem Zusammenhang muss auf meine letzte Veröffentlichung über die Flora von Lunz hingewiesen werden (Palaeontographica B, 89, 1949), in der die Mehrzahl der bisher von Lunz bekannten Bennettiteen- und Cycadeen-Fruktifikationen ausführlich beschrieben worden sind. Darunter ist eine Art von *Dioonitocarpidium*, ein Sporophyll vom *Cycas*-Typus. Es kann daher keinem Zweifel unterliegen, dass beide Formen des Cycadeen-Sporophylls von gleichem Alter sind, wenigstens nach dem, was wir heute darüber wissen. Dr. THOMAS zeigte ferner die Skizze einer Samen enthaltenden Frucht von *Bennetticarpus Wettsteini*. Auch dies Stück ist mit manchem anderen der gleichen Art in der genannten Arbeit abgebildet. Andere Stücke lassen erkennen, dass die Samen auf mehr oder weniger langen Stielen sassen. Die Interseminalschuppen sind sehr klein; ihre Zahl ist demzufolge sehr gross. Sie bilden einen völlig geschlossenen Panzer um die Frucht. Wir haben ihn an mehr

als zehn Stücken mazeriert, aber niemals etwas gefunden, was als Mikropyle gedeutet werden könnte. Jede Interseminalschuppe trägt in der Mitte eine kegelförmige Verdickung, die in der Regel abgebrochen ist. Dann entstehen an ihrer Stelle die Löcher, die auf einem der gezeigten Bilder zu sehen waren. Mit Mikropylen haben sie nichts zu tun. Mir scheint, dass die Unterschiede zwischen der fertilen Region der Bennettiteen und derjenigen der Cycadeen doch recht gross sind, besonders wenn man so eigenartige Formen wie die gleichfalls von LUNZ bekannte *Westersheimia* (siehe oben KRÄUSEL) berücksichtigt. Denn hier finden wir ein gefiedertes Organ (in Zusammenhang mit dem tragenden Stamm), dessen „Fiedern“ jede für sich eine vollständige „Frucht“ von dem für die Bennettiteen kennzeichnenden Bau darstellen. Es mag dennoch richtig sein, dass beide Gruppen phylogenetisch gemeinsamer Herkunft sind, doch sind meines Erachtens Formen, die als ihre Ahnen in Betracht kämen, bisher noch nicht bekannt. Die *Corytospermaceen* und ähnliche Formen scheinen mir den *Caytoniales* näher zu stehen, als den Bennettiteen und Cycadeen.

W. ZIMMERMANN: Der Grundgedanke, dass die *Bennettitales* und *Cycadales* auf eine gemeinsame Grundform zurückgehen, scheint mir berechtigt, auch wenn man den reich verzweigten und nicht in einen Zapfen zusammengezogenen *Cycas*-Typ für primitiver hält.

T. M. HARRIS: The stomata of cycads and *Bennettitales* are of contrasted types, and no intermediate form has so far been found. I suggest that where the organs of two plants can be understood in terms of one another, they can be regarded as related. Where an intermediate must be invented, this is doubtful. Where two intermediates must be invented, they are better regarded as unrelated.

J. HSÜ (Lucknow)

New Information on Homoxylon rajmahalense SAHNI

Homoxylon rajmahalense is one of the most interesting petrified fossils described by Profes-

sor B. SAHNI (1932) from the Rajmahal Series of India. As the fossil locality is not known, there is some doubt about the geological age. The original specimen is a piece of secondary wood lacking both inside and outside. The interest attaches solely to growth rings and the peculiar tracheids. These tracheids show various types of pitting on their radial walls, including both scalariform and multiseriate pitting. The wood closely resembles that of certain dicots without vessels, such as *Trochodendron* and *Drimys* which are placed in, or near, the *Magnoliaceae*. Later on, one of SAHNI's students, K. M. GUPTA, suggested that a comparison was possible with the *Bennettitales*, to which SAHNI (1938) agreed.

The present material was collected in 1948 by SAHNI and others in a party, including myself, at Amarjola—a classic locality in the Rajmahal Hills of the Amarapura District of Bihar—and believed to be about Middle Jurassic in age. It consists of at least three rather poorly preserved petrified stem fragments. The specimens are crumbly, but after boiling in balsam they were quite easy to cut.

The biggest one is 18 mm wide and 4.6 cm long. It is complete, having a central pith, a compact zone of secondary xylem and phloem and a well-preserved bark of periderm. It is younger than SAHNI's specimen; the original specimen must have come from an older and lower stem.

In transverse sections there is a large pith with conspicuous but small, sclerotic nests. Around this is a compact zone of secondary wood composed of tracheids and rays only. The xylem shows nine clear growth rings, each of about twenty layers of tracheids. The late woods are more strongly developed than the early ones, but consist of slender tracheids throughout. Radial longitudinal sections show the characteristic pitting of the tracheids, ranging from scalariform to multiseriate and bordered. The ray field pits are 1–6 in number and also bordered. The marginal ray cells are usually larger. Tracheids seen in tangential longitudinal sections reach a length of about 2 mm. Pits are

very rare on the tangential walls. The uniseriate rays are the commonest, but biseriate rays also occur, and I have also seen a few triseriate ones. In almost all the details of the secondary wood, the present fossils agree perfectly with *Homoxyylon rajmahalense*. This investigation thus removes the doubt about the geological age of the original specimen.

In the pith the cells of the sclerotic nests are slightly more elongated than the others. Their walls are thicker and simple-pitted.

I have not yet succeeded in recognizing clearly the primary xylem. Presumably this is more or less endarch. A few masses of smaller cells are lying around the inner border of the xylem around the pith. These probably are the primary xylem groups. But I have not yet had a good longitudinal section through any of these groups.

The cambium is not well preserved, but the phloem is. It, too, shows about nine growth rings. The periderm is lying next to the phloem. It consists of separate arcs of corky tissue. I have not found any leaf traces or other kinds of tissues outside the periderm.

As regards the nature and classification of *Homoxyylon rajmahalense* the present specimens do not exclude affinity with either the *Magnoliaceae* or the *Bennettitales*. I hope that further investigations will yield some conclusive facts.

At Amarjola no leaves resembling those of dicots have so far been discovered in association with *Homoxyylon*. Therefore, this genus probably belongs to the *Bennettitales*. If so, the stem fragments might have come from a woody stem of *Williamsonia*. Actually, *Williamsonia* and *Philophyllum* are very abundant at this locality. In contradistinction to our specimens, stems of the *Bucklandia* type, also found at Amarjola, are covered with leaf bases, but *Homoxyylon* might possibly represent portions of such stems which have lost their leaf bases through cork formation.

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SESSION 7

July 19th, 9—11 a. m., Attendance: 45 members

Chairman: J. WALTON

SUBJECT:

Paleobotanical Technique

J. WALTON (Glasgow)

Level Table for Use in Preparation of Peel Sections

In making peel sections it is usual, after the etching process and the application of the plastic material in liquid form, to prop up the block of material so that the film surface is as level as possible. This usually takes some time and can only be done approximately. As a result the film is often thicker on one side than on

the other and in most cases where the film comes to the edge of the block there is a thicker marginal region all round. To avoid these faults I find the following procedure satisfactory.

The specimen is faced with the section-surface downwards on a steel plate which has three levelling screws. By using a spirit level the plate can be accurately levelled. An enclosure of plastic sheet is placed round the specimen, the plastic sheet being so cut that

its two edges are parallel. Plaster of Paris is then poured over the specimen and the enclosure is completely filled, the top surface of the plaster is levelled with a straight edge and allowed to set.

The specimen is now embedded in a roughly cylindrical block of plaster, the upper and lower surfaces are parallel.

In making a peel from the surface the plastic solution is allowed to extend over the surface of the plaster so that any thick edge is formed over the plaster and not on the surface of the section. The plaster is placed on the levelled metal sheet to dry and by this means an evenly thick section can be prepared.

If sections have to be prepared from a number of small specimens of the same type and material (same etching rate) they can be embedded in one block of plaster so that sections can be prepared from them simultaneously. This effects considerably saving of time and handling.

T. M. HARRIS (Reading) *Palaebotanical Technique*

The Middle Jurassic outcrop of Yorkshire provides several hundred localities where determinable plant fragments can be found. Most of these are small exposures in stream sections or in gulleys caused by farm traffic.

These outcrops can, ideally, be localised to about 20 m by the help of a large scale map (6 inches to 1 mile) and have been designated by their latitude and longitude. Unfortunately the maps are by no means everywhere accurate, but no more precise localisation seems possible without the use of surveying methods.

The material collected consists of thin coal seams, shales and sandstones with plant fragments. As a rule about 1 kg of rock is collected and macerated by the action of concentrated nitric acid (without potassium chlorate). Maceration should be complete in a week but a longer period does not harm as the acid becomes weaker. The commonest fossils are cuticles of *Equisetites columnaris* and small fragments of charcoal, but varying numbers of leaf cuticles,

seeds and *Selaginella*-like megaspores are found. Small spores occur in abundance, but have so far been neglected.

Results. The plant-bearing "Estuarine Series" consists of four deltaic phases separated by three marine ones. Plants had been recorded from three of the deltaic phases only, but all seven yield determinable microfossils. In tracing the flora through the series one surprising feature noted is a change from the lower stages to the middle and then a partial return at the top to a flora more resembling the older one.

The flora of these beds with small fragments is very different from that of classic localities; for example *Ptilophyllum pecten* and *P. pectinoides* are rather rare, but other species such as *Araucaria*-like leaves never yet found represented as a twig on a hand specimen are abundant and widespread. Megaspores of several unknown lycopods are also frequent. It is suggested that the classic localities represent the plants growing beside lagoons in the deltaic swamps while the fragment-bearing beds represent in part an otherwise unknown inland flora. It must be emphasized that only those elements of the flora with fairly thick cuticles are represented in such macerations.

Various difficulties were met. Derived fossils from the Carboniferous are occasionally met but can be detected; there is however no obvious way of recognizing derived fossils from a slightly older stage in the Jurassic. Recent material of plants and insects often occurs in small amounts, but this too can generally be recognized. It is suggested that the best safeguard against these and similar accidents is to return to the locality which has yielded a surprising result and to repeat the maceration, only regarding the result as fact if it is confirmed.

R. KRÄUSEL (Frankfurt am Main) *Neue Präparationsmethoden*

In meinem früheren Vortrag (p. 574) habe ich darauf hingewiesen, wie wichtig es ist, bei der Untersuchung tertiärer Laubblätter mor-

phologische und anatomische Analyse zu vereinigen. Die erste muss dabei auch den feineren Nervenverlauf berücksichtigen, der auch an rezenten Blättern meist schlecht oder garnicht zu erkennen ist. Man muss sie daher bleichen, aufhellen und nachträglich färben. Verschiedene Bleichmittel wurden angewandt (u. a. Kali- oder Natronlauge), am geeignetsten erwies sich Wasserstoffsuperoxyd (H_2O_2), während zum Färben Safranin benutzt wurde. Die so behandelten Blätter werden auf Glasplatten montiert. Als Einbettungsmittel bietet Glycerin-gelatine vor anderen Mitteln (Kanadabalsam) mancherlei Vorteile, u. a. wird der Gang der Präparation erheblich vereinfacht und beschleunigt. Als „Deckglas“ benutzen wir Zellulosefilme von der Art der in der Photographie angewendeten. Namentlich grössere oder dickere Blätter lassen sich mit dem biegsamen Film viel leichter bedecken als etwa mit einer Glasplatte. Auf diese Weise erhält man ein für Vergleichszwecke sehr geeignetes „Glaserbar“.

Das gleiche Verfahren ist auf fossile Blätter anzuwenden, wenn sie aus dem Gestein, etwa einer torfigen oder lockertonigen Schicht, durch Schlämmen frei gemacht werden können. Da sie oft recht brüchig sind, ist namentlich beim Bleichen grosse Vorsicht am Platze. Beim Herausheben unterfängt man sie mit einer Glasplatte.

Wo die kohlige Blattsubstanz dem Gestein fest aufsitzt, kann das Blatt vermittelst eines Abziehfilms nach J. WALTON abgehoben und weiter in der gleichen Weise wie oben behandelt werden. Solche Präparate zeigen nicht nur alle Feinheiten der Nervatur, sondern ebenso den anatomischen Bau der Epidermen bzw. Kutikulen. Wenn erforderlich, können sie auch noch mit SCHULZE'schem Mazerationsgemisch usw. behandelt werden.

Durch dieses Verfahren werden auch etwaige Mikroreste sichtbar, die auf den tertiären Blättern sitzen. Hierher gehören u. a. die scheibenförmigen Gebilde, die bisher meist den Microthyriaceen zugeschrieben wurden, zum Teil aber Algen sind (*Phycopeltis*; vergl. HÖCK, KIRCHHEIMER). Auch was kürzlich ISABEL

COOKSON unter verschiedenen Art-, ja sogar Gattungsnamen aus Australien beschrieben hat, sind zum grossen Teil nur verschiedene Entwicklungsstadien einer solchen Alge.

Nähere Angaben über Arbeitsgang usw. finden sich in meinen „Paläobotanischen Untersuchungsmethoden“, 2. Aufl., Jena 1950.

A. S. FOSTER (Berkeley, Calif.)

Techniques for the Study of Venation Patterns in the Leaves of Angiosperms

The difficulties of correctly determining and classifying the fossil leaves of angiosperms present serious problems to the paleobotanist. Comparisons with extant species based solely on leaf form are often misleading because of the polymorphism of the foliar organs in many plants. On the contrary, a precise and scientific approach to the problem requires a search for more critical diagnostic structural features which are likely to be evident in fossil material. One of such morphological characters is the foliar venation. But the proper use of this character for diagnostic purposes in turn depends upon a comprehensive knowledge of the types and degree of variation in the venation patterns of living angiosperms. Since unfortunately this subject has never been broadly explored by the morphologist, there is great need for assembling extensive collections of permanent slides of venation patterns of a wide range of angiospermous genera. Such "slide herbaria" would prove invaluable to the paleobotanist in his difficult task of interpreting and classifying fossil leaf specimens. The successive steps in the technique used by the writer for studying venation patterns may be briefly summarized:

1. *Clearing* in 5 % NaOH. Small leaves may be cleared *in toto*; large leaves should be subdivided to include representative portions of the venation. Removal of the pigments with heat provided by an electric oven (25° C) requires but a few days for many objects. Preliminary bleaching with "Eau de Javelle",

followed by NaOH, may be necessary in some cases.

2. *Dehydration.* After thorough washing in distilled water, the material is dehydrated in successive grades of alcohol (50 %, 95 %, 100 %).

3. *Staining.* A 1 % solution of safranin, composed of equal volumes of absolute alcohol and xylene, yields consistently good results. Sufficient staining is rapidly accomplished (10–20 min.) and destaining secured by either a mixture of absolute alcohol-xylene or acidified alcohol. (For other stains valuable for cleared leaves cf. MORLEY in *Stain Technology*, 24: 231–235, 1949). When satisfactory differentiation of the vascular system is attained, place the specimens for 15–30 min. in pure xylene.

Mounting. "Clarite", because it dries rapidly, is recommended in preference to Canada Balsam. The use of large slides and cover glasses (7.5 × 5 cm) permits mounting of entire small leaves or generous portions of larger organs. Place slides on an electric slide warmer until they are thoroughly dry.

Cleared stained leaves of a series of angiospermous genera will be exhibited to illustrate the results of this technique.

SUZANNE LECLERCQ and M. DISCRY (Liège) *Preparation of Fossil Plants in Transparent Mounting*

Fossil plants showing structure and impregnated with an opaque mineral substance have been mounted in transparent plastic material and, after polishing, observed in strong reflected light.

The embedding of the specimens has been successfully tried out by two methods: the first with a thermo-plastic powder requiring a mount press equipment; the second with a copolymer of styrene and polyester of allyl which solidifies in ambient heating.

The use of transparent plastic is particularly suitable for establishing the correct level at which the enclosed specimen has to be cut, ground, or polished.

This paper was read by Professor LECLERCQ.

K. MÄDLER (Hannover)

Über die Möglichkeiten einer planmässigen morphologischen Analyse der dikotylen Blätter

Bei der Bestimmung tertiärer Laubblätter entstehen dadurch Schwierigkeiten, dass in den meisten Fällen die erforderlichen Grundlagen, insbesondere die Vergleichsmöglichkeiten mit den rezenten Blättern fehlen. Vorhandene Angaben sind in der Literatur verstreut und schwer zugänglich. Die Kutikularanalyse setzt zwar die Kenntnis der Anatomie der rezenten Blätter voraus, aber jede Bestimmung fossiler Formen wird zunächst von den leichter zugänglichen morphologischen Merkmalen ausgehen. Dieses Verfahren wird aber dadurch erschwert, dass gleiche Blattformen in verschiedenen Familien vorkommen. Wir müssten daher zur Erleichterung der Bestimmung fossiler Blätter Listen der konvergenten Blattformen in der rezenten Flora haben. Solche Listen können aber nur wertvoll sein, wenn sie nicht nach dem äusseren Augenschein aufgestellt werden, sondern nach einer Methode, die ich als „Planmässige morphologische Analyse“ bezeichne. Diese nimmt nach dem Prinzip der fortlaufenden Gliederung eine Einteilung der Blattformen nach den Hauptmerkmalen: Grundform, Berandung, Nervatur, Spitze, Grund, Stiel, Grösse und Textur vor, da diese an fossilen Blättern ebenfalls am leichtesten erkennbar sind. Die so ermittelten Merkmale werden nach einem bestimmten Schema in eine Karteikarte eingetragen. Diese Karten werden in ein Karteisystem so eingeordnet, dass sich die konvergenten Formen an einer Stelle zusammenfinden. Hat man konvergente Formen auf diese Weise festgestellt, so können diese nach weiteren morphologischen Merkmalen so weit getrennt werden, bis nur noch vollkommen übereinstimmende Formen übrig bleiben, die nun noch nach anatomischen Unterschieden (Epidermisstruktur, Einlagerungen im Mesophyll usw.) getrennt werden können. Da alle diese Merkmale auch an gut erhaltenen fossilen Blättern (nicht Blattabdrücken!) erkennbar sind, so könnte man mit dieser Methode den

Arbeitsgang der Bestimmung fossiler Blätter wesentlich vereinfachen.

Es konnte hier nur der Weg gezeigt werden, den wir gehen müssten, um zu dieser Vereinfachung zu gelangen. Da in Deutschland heute kein Institut in der Lage ist, eine derart umfangreiche Arbeit durchzuführen, wird eine Veröffentlichung des Karteisystems angestrebt.

Exhibits

The exhibits of specimens and microscopic slides of fossil plants arranged in an adjoining room were inspected by the members of the Section.

SESSION 8

July 19th, 2.15—5.30 p. m., Attendance: 45 members

Visit to the Paleobotanical Department of the Natural History Museum at Frescati

Chairman: H. HAMSHAW THOMAS

SUBJECT FOR DISCUSSION:

The Present Position and Needs of Paleobotany

The discussion was opened by Professor T. G. HALLE. Other members taking part in it were H. N. ANDREWS, C. A. ARNOLD, E. S. BARGHOORN, MARY CALDER, W. N. EDWARDS, W. GOTHAN, T. M. HARRIS, O. A. HØEG, SUZANNE LECLERCQ, N. W. RADFORTH, SAVITRI SAHNI, O. H. SELLING, R. SITHOLEY, H. HAMSHAW THOMAS, and J. WALTON.

It was resolved that an International Association of Paleobotanists should be established to promote the advance of Paleobotany with-

out interfering with existing institutions. To that end an organizing committee was formed, consisting of W. N. EDWARDS (as convener), H. N. ANDREWS, R. FLORIN, W. GOTHAN, and R. SITHOLEY as members.

It was also resolved to place a wreath on the grave of Professor ALFRED GABRIEL NATHORST in Stockholm on November 7th, 1950, the centenary of his birth, in memory of his great achievements in Paleobotany.

SESSION 9

July 20th, 9 a. m.—1 p. m., Attendance: 45 members

Chairmen: W. J. JONGMANS and P. CORSIN

SUBJECT:

Paleozoic and Mesozoic Floras: General Distributional Problems

W. GOTHAN (Berlin)

Allgemeine Verbreitung der paläozoischen Floren mit Ausblicken auf die mesozoischen

Ein Überblick der Verbreitung der Floren im Devon zeigt, dass trotz lokaler Eigentümlich-

keiten im Unter- und auch noch Oberdevon im ganzen eine einheitliche, physiognomisch ähnliche Flora auf der Erde existiert hat, soweit die bisherigen Funde zeigen. Auch im Unterkarbon ist es im ganzen bis auf Einzelheiten noch so, erst um die Wende des Karbon-

Perm tritt, offenbar im Zusammenhang mit den jungkarbonischen Vereisungen in den südlichen Gebieten, eine Sonderung in zwei grosse Florenprovinzen ein, die man als arkt- und antarkto-karbonische Floren bezeichnet hat. Beide Karbongebiete lassen eine zirkumpolare Anordnung erkennen; die antarkto-karbonische, fast bis zum Südpol verfolgte ist als recht einheitlich zu erkennen (*Glossopteris*-Gondwana-Flora). Bei der nördlichen Flora ist eine Gliederung in 3 Teilprovinzen zu bemerken, die unter dem Namen euramerische, Angara- und Cathaysia-Flora bekannt sind. Bei der erstgenannten ist eine Sukzession der Flora vom Unterkarbon (auch Oberdevon) bis zum älteren Perm zu beobachten, mit Kohlenbildung namentlich im Westfal; bei den drei anderen fehlt die Verbindung in den Schichten zwischen Unterkarbon und Permo-Karbon. Man kann daher dort die pflanzen- und kohlenführenden Schichten nur mit den permo-karbonischen des euramerischen Gebiets vergleichen. Das euramerische Gebiet ist ziemlich einheitlich, bis auf lokale Differenzen einzelner Teilgebiete. Das Angaragebiet führt einige Sonderformen sowie Einwanderer der südwärts gelegenen Gondwana-Flora, aber fast nie *Glossopteris* selbst und führt als euramerisches Element besonders *Calopteris*-Arten. Die Cathaysia-Flora (von Korea bis hinunter nach Sumatra, neuerdings mit Spuren in Neuguinea) ist im ganzen wieder euramerisch, aber mit Sondertypen wie *Gigantopteris*, *Tingia*, *Emplectopteris* etc., und ist auch im südwestlichen Nordamerika vertreten. Trotz grosser lokaler Annäherung der Floren mischen sie sich im allgemeinen nicht. Nach Norden sind einzelne Gondwana-Formen wie *Phyllothea* und *Noeggerathiopsis* in die Angara-Flora vorgestossen; nach Süden hat man in mehreren Gebieten Vorstösse der euramerischen Flora bis nach Südafrika (Süd-Rhodesien) und in geringem Masse nach Portugiesisch-Ostafrika beobachtet (Tete-Becken nach C. TEIXEIRA), aber nicht in dem Grade wie in Süd-Rhodesien. Die von R. ZEILLER nach LAPIERRE von dort irrtümlich angegebene rein euramerische Permo-Karbon-Flora ist nach wie vor zu streichen.

Die euramerische Flora reicht im allgemeinen sowohl in Nordamerika als in Nordafrika bis zum 30° n.Br. Südliche Ausläufer sind aus Guatemala, Kolumbien und Nord-Brasilien (*Psaronius brasiliensis*) bekannt. Die Angabe einer „*Alethopteris*“ *branneri* als karbonisches Element aus dem Staate Bahia (Nord-Brasilien) hat sich als eine *Lacopteris* herausgestellt (nach GOTHAN). In Paraná ist besonders *Sphenophyllum oblongifolium* (wie im Tete-Becken in Südafrika) als euramerischer Vorposten bemerkenswert. Ausserdem hat ZEILLER aus Süd-Brasilien ein schlecht erhaltenes *Lepidodendron* und *Lepidophloios* angegeben; *Lycopodiopsis* scheint eine Sache für sich zu sein. Eine von E. W. BERRY aus den peruanischen Anden angegebene *Pecopteris* müsste erst genauer untersucht werden, ebenso die *Pecopteris*-Formen in Paraná (und vielleicht ähnliche in Ost-Indien!). Eine weite Lücke klafft sowohl in Südamerika wie in Afrika zwischen diesen südlichen Vorposten und den südlichsten euramerischen Vorkommen. So ist gegenüber den im vorigen Botanischen Kongress von 1935 vorhandenen Kenntnissen nur ein unerheblicher Fortschritt zu verzeichnen. Klimatische Fragen wurden nur nebenher berührt.

Für die Post-Gondwana-Flora sind im Gondwana-Gebiet als kennzeichnend besonders die *Dicroidium*-Arten („*Thinnfeldia*“), *Stenopteris elongata* und Verwandte zu bezeichnen, sowie z. T. Glossopteriden ohne Maschenaderung (*Linguiifolium* ARBER). Die Residuen der Gondwana-Flora im Rhät von Tonkin sind extraterritoriale Überbleibsel ähnlich den heutigen „lebenden Fossilien“. In der Folgezeit macht sich allmählich immer mehr die weltweite Ähnlichkeit der Jura-Flora bemerkbar, die auch in der Unterkreide verschiedener Gebiete ähnliche Züge aufweist (*Weichselia*, *Matonidium*). Die darauf folgende, die Tertiärflora einleitende kaenophytische Zeit fällt ausserhalb der vorliegenden Betrachtungen.

Discussion

W. N. EDWARDS: In connection with the supposed occurrence of northern lycopods in

the southern hemisphere *Glossopteris* flora, a re-examination of specimens from Brazil and South Africa originally referred to *Sigillaria Brardi*, *Lepidodendron*, and *Lepidophloios* shows that there is no satisfactory reason for referring these specimens to any of these genera. A critical study of the relevant literature also reveals the extremely slender basis for the original identifications. On the contrary, all these lycopods appear to be different parts, or different states of preservation, of one and the same general type of lycopod, falling into the genus *Lycopodiopsis* RENAULT.

W. GOTHAN: To the remarks of Dr. EDWARDS I must add that in my paper I did not refer to *Lepidodendron* and *Lepidophloios*, although I have mentioned them in my draft. I am glad to hear that these genera will now be removed, and that Dr. EDWARDS is of the same opinion as I am with regard to the so-called "*Sigillaria Brardi*" from Gondwana land. I wish to thank Professor JONGMANS for some geographical corrections.

T. G. HALLE: To Professor GOTHAN's clear and concise summary of the distribution of the Late Paleozoic floras I only wish to add some remarks on the subject of terminology. In speaking of the *Gigantopteris* flora of East Asia it is important to bear in mind the exact meaning of the term in relation to time. This also applies to the *Glossopteris* flora, which name is sometimes loosely used as equivalent to the Gondwana flora. As every paleobotanist knows, the *Glossopteris* flora only corresponds to a certain phase, broadly speaking the Stephanian - Permian, of the development of the Gondwana flora, while the latter name covers not only the Late Paleozoic, but also the Early Mesozoic floras of Gondwana land as conceived by SUESS. The term "Angara flora" is similarly used for the whole sequence of contemporaneous floras of the Siberian Angara Land of SUESS. Unfortunately, we have no special name for that particular stratigraphical division of the Angara flora which is characterized by various species of *Callipteris*, and by a number of peculiar genera. Such a term, chosen from one of these

genera, ought to be introduced, but only after careful consideration. In the Late Paleozoic floras of East Asia three more or less well-defined phases can be distinguished, in ascending order: 1. The upper Westphalian-Stephanian flora of typical Euramerican aspect, developed especially in the Kaiping basin. 2. The uppermost Stephanian-Lower Permian *Gigantopteris* flora, characterized by several peculiar types and by an increase of the American elements. This is the flora of NORIN's Shihhotse Series of Central Shansi and of the equivalent beds in the Kaiping basin, in Korea, and in Sumatra. In Shansi there is a distinct difference between a lower part with *Gigantopteris Whitei* (= *Cathaysiopsis Whitei* KOIDZUMI), and an upper part with *G. nicotianaefolia*. In Sumatra only the lower of these divisions is known. 3. The flora, of Angara aspect, discovered by G. BEXELL in the Nanshan, and its possible equivalent in NORIN's Shihchienfeng Series in Shansi. For the whole succession of Paleozoic floras in East Asia I have (1935) proposed the term the Cathaysia flora, which was named, in analogy with the Gondwana and Angara floras, after the Late Paleozoic land-mass in East Asia distinguished by GRABAU. It now only remains to give a special name to the most distinctive, Permian, division of the Angara flora mentioned above. This would give us a consistent and parallel nomenclature, not only for the whole sequences of floras in the three old continental areas considered here, but also for the particular phases of these floras, which—in very different degrees—differ most markedly from the typical Euramerican flora of the same age and are accordingly most often discussed.¹

J. M. SCHOFF: There are plenty of plant microfossils in the Upper Paleozoic beds of the southern hemisphere. I believe the best comparison of floras of Gondwana land and those of the

¹ G. KOIDZUMI (1934, 1936) has divided *Gigantopteris* into five subfamilies (?) and eight genera! A subdivision is probably needed, and has been discussed by competent paleobotanists, but has been postponed for good reasons. KOIDZUMI's classification—which is not based on any fresh arguments—is utterly indiscriminate and absurd, and can only be explained by lack of experience in paleobotanical work. (Note added after the meeting.)

northern hemisphere will be derived through study of this material.

W. J. JONGMANS (Heerlen)

Carboniferous Floras round the Paleozoic Mediterranean

In the Silurian and Devonian floras there is no possibility to distinguish differences that might indicate dissimilarities of climate. The floras of the Lower Carboniferous, as far as they are known, all belong to comparable types. There may be some differences between the American and European floras, but they seem to have a more or less local character.

During the Upper Carboniferous or Pennsylvanian we find other conditions. We divide the Pennsylvanian into

Namurian A, B, C
Westphalian A, B, C, D
Stephanian A, B, C
Autunian.

The Autunian is a more or less transitional upper division, comprising the Autunien, the Rotliegendes and the upper parts of the American Dunkard. The conception of the Dunkard is rather obscure. It is possible that some of the lower parts belong to the Stephanian, and some of the lowermost parts may even belong to the Westphalian D. The question of the stratigraphical position of the Dunkard must be reconsidered very carefully.

During the Namurian and the Westphalian, the floras throughout the world are very uniform.

It has been discussed very often whether this Euramerian flora is to be considered tropical or subtropical, or perhaps even temperate. If it were temperate there ought to be a part of the world in which we could expect subtropical or even tropical floras. If it were subtropical it must be bounded in the North and the South by a more temperate flora, since as we shall see later on, the Euramerian flora is in contact with the Gondwana flora at different places toward the end of the Stephanian and during the Autunian.

With the intention of seeking such a difference, I have undertaken to look round the present Mediterranean. I studied the floras of Spain, the Donetz basin, Turkey, Algeria (coalfield of Colomb-Bechar and, south of this, that of Sfaia and, still further to the South, that of Djebel Mezarif), French Morocco (coalfield of Djerada, and the basin of El Mnizla on the southern side of the Atlas mountains). These basins contain floras which belong to the same Euramerian type; so we see that this flora was present even south of the Carboniferous Tethys.

This is also the case in China, in the Kaiping basin, during the Namurian and Westphalian. It is almost certain that similar floras of still undetermined age occur in the northern part of Brazil (round Teresina) and in Argentine (southern part).

This conformity changes in the highest part of the Stephanian and in the Autunian.

In East Asia the Cathaysia flora develops. This flora contains many Euramerian types, especially in the beginning. Besides these, numerous special types occur, most abundantly in the upper parts of the strata. One of the most important genera is *Gigantopteris*, which occurs also in the *Gigantopteris* beds in the United States.

The Cathaysia flora is best known from China by the important work of T. G. HALLE. It has also been found in Malakka and in Djambi (Sumatra). The Djambi flora shows more similarity with the Euramerian flora and must be considered Upper Stephanian. The Chinese flora belongs to the Upper Stephanian and the Autunian.

A further type of flora is found in north-eastern Russia and Siberia, the Kusnetzki or Angara flora. This belongs partly to the Stephanian and partly to the Autunian. On several occasions *Glossopteris* has been mentioned as an element of this flora. However, it is not certain whether this is right, as many of the specimens and determinations are doubtful. At all events this flora contains many elements which indicate that it has been growing under a cooler climate. A flora which can be compared with it is the Hermit flora in the United States.

It is extremely interesting that in the upper part of the Autunian this flora spread to the South, where it overlies the upper layers of the Cathaysia flora, as has been proved by HALLE from G. BEXELL's collections.

The most important special flora is the Gondwana flora found in Australia, India, South Africa, the Antarctic, the Falkland Islands and South America. This flora has been growing under a rather cold climate, but this does not necessarily mean that it was a glacial flora.

It is extremely interesting that the Stephanian Euramerian and the *Glossopteris* flora meet in South America and South Africa. G. LUNDQUIST described this mixture from South America, J. WALTON from Rhodesia, and C. TEIXEIRA from the Zambesi region.

This seems to prove that the Euramerian flora had an extension from western Europe and the United States in the North to Brazil and southern Rhodesia in the South, and that it shows the same type of flora over the entire region. In the older part of the Pennsylvanian it has also extended over Asia, especially China.

It is clear that it cannot have been a tropical or subtropical flora, but one growing in a wet and temperate, but rather warm and uniform climate without marked differences between winter and summer, so that it could grow also in the most southern parts where it met with the *Glossopteris* flora. No trace of a special tropical or purely subtropical flora can be found. There is no room for it. Over the whole extension this flora has been practically uniform.

The same is true of the Cathaysia flora. I found in New Guinea a flora composed of Cathaysia elements and *Vertebraria*. This proves that the Cathaysia flora also reached the northern borders of the Australian *Glossopteris* flora.

It is remarkable that some of the regions containing the *Glossopteris* flora are today so near to regions containing Euramerian or Cathaysia floras. It may also be asked why the *Glossopteris* flora is in some cases found in parts of the present southern continent which lie so near the equator as India.

The whole of the *Glossopteris* regions formed one big block which was lying far more to the South in Carboniferous times. Afterwards this block fell into different parts. India moved to the North and was pressed against the Asiatic continent and influenced the folding of the present Altai and Himalaya mountains. By this pressure some of the easternmost parts of the Cathaysia region, Malakka and western Indonesia, which have probably been lying more to the North, were pushed southwards into their present positions.

Australia and New Guinea, the latter of which also contained elements of the Cathaysia flora, were moved in a northeastern direction. It is thus possible to understand the present position of these so divergent portions of East Asia.

Discussion

J. M. SCHOFF: I have long thought that the best evidence bearing on the controversial question of continental displacement was illustrated by the occurrences Professor JONGMANS has discussed in India and southeastern Asia. I wonder if he has formed an opinion about the time of the displacement he has indicated?

W. J. JONGMANS: According to A. DU TOIT the northward movement of parts of the Gondwana block began soon after the Pennsylvanian. In Mesozoic time, however, it was relatively slow and irregular. In some places, especially in southeastern Asia, the southern and northern blocks may possibly have been very close together, or perhaps even connected, in Early Mesozoic time, while in the Jurassic the Tethys widened, and the distance between the continental blocks thus became rather large. At the end of the Mesozoic the Indian-Australian blocks must have been rather close to the Asiatic block. The principal movement must have taken place in the Tertiary, when the Altai and Himalaya mountains originated. It seems to me that Du Toit's scheme gives a reasonable explanation of several paleobotanical problems.

T. G. HALLE: The so-called Gondwana elements in the Permian Angara flora of Siberia—in my opinion overestimated by ZALESKY—are still often explained by assuming immigration from India. B. SAHNI mentioned not so very long ago that D. N. WADIA's observations in the Kashmir region seem to indicate the existence of an archipelago, which might have served as a bridge across the Tethys. As I pointed out in 1937, the idea of an immigration from India can in any case not be entertained by those who accept WEGENER's explanation of the Late Paleozoic glaciation in the peninsula on the basis of his theories of continental drift. The fundamental feature of his explanation is that the Indian peninsula was at the time of the glaciation situated at no great distance from the supposed Late Paleozoic position of the South Pole, i.e., somewhere near Madagascar. But in that case the peninsula could not have come into contact with the continent of Asia until long after the Permian Angara flora became extinct. Even apart from WEGENER's views, it is evident that the distance between Angara land and the Indian peninsula was much greater in Carboniferous-Permian times than it is now. As has often been remarked, the immense post-Permian folding and overthrusting evidenced by the mountain ranges of the Himalayas and Central Asia must have resulted in horizontal contractions on a very great scale. The immigration hypothesis must reckon with the distance dividing the two floras before these events. The contraction has even been conceived as amounting to something approaching the whole width of what in the Late Paleozoic may have represented the tropical zone of this region! According to this seemingly phantastic idea, the Angara flora would represent the missing northern counterpart of the southern temperate Gondwana flora. Without going as far as this, geological facts undoubtedly constitute a serious obstacle to the hypothesis of a migration of Permian plants from India to Angara land.

J. WALTON: In South Africa there is some evidence of fluctuations in climate in the Rho-

desian and Tanganyikan area. In Tanganyika a pure *Glossopteris* flora is found while further south in southern Rhodesia a mixed flora occurs at Wankie.

W. J. JONGMANS: Some species of the Gondwana region were certainly able to move more to the North than others, which would result in an irregular contact line between the two floras.

H. HAMSHAW THOMAS: Attention should be paid to the climatic conditions of the whole world at a time when they must have been quite different from those of the present day. The conditions of the atmosphere to produce the very heavy rainfall of which we have evidence necessitate a very wide belt of country comprising equatorial and subequatorial zones, with heavy cloud, little or no direct sunshine and rapid atmospheric circulation; in the polar regions there could be heavy snowfall. I wish to draw the attention of paleobotanists to the papers of the English meteorologist G. SIMPSON, whose conclusions founded on Physics and Mathematics are most important in discussing the distribution of plants.

W. J. JONGMANS: I quite agree with Dr. THOMAS's opinion of the climate in which the Euramerian flora lived.

E. S. BARGHOORN: Dr. JONGMANS has pointed out the puzzling fact that there is little taxonomic (hence phytogeographic) difference between the Late Carboniferous floras of north-western Europe and those occurring south of the Mediterranean. Existing plant communities show an extreme difference in these two areas today; a difference assignable to ecological relations imposed by climate and by latitudinally controlled climatic factors. Barring special conditions of topography or orographic influences on climate the question arises why climatic zones of the Late Paleozoic did not impose distinct phytogeographic zones in the past as they do today. It may be argued that on a spherical and rotating earth with its existing relation to the sun such zones must exist. We have no valid reason for invoking special astronomical explanations for our phytogeographic problems of the past, and it would seem more reasonable

to seek a biological explanation. A tempting explanation of the uniformity of latitudinally widely separated floras of the Paleozoic lies in the possibility that physiological response to diverse ecological conditions had not yet evolved to a high level of sensitivity. Hence morphologically and anatomically similar plants (therefore taxonomically uniform) perhaps actually grew under very diverse climatic conditions. Organic evolution is well featured by a correlation between the development of structures and physiological demands set by the environment. It is suggested as a theoretical possibility, therefore, that floristic similarity in Paleozoic floras which are geographically separated may not actually indicate similarity of environment. The fact that climatic zones of the earth today can be roughly defined in phytogeographic terms does not necessarily imply that climatic zones of the distant past can be delimited by floristic correlations. Sensitivity to the physical environment has possibly evolved at a rate as rapid as morphological change. This argument is not offered as a criticism of facts but merely as a theoretical explanation of a phytogeographic enigma.

W. GOTHAN: The subject of Professor JONGMANS' paper covers not only the Mediterranean region, but almost the whole world. It is most satisfactory to learn something new about the North African coal field. I am glad of the recent progress along this line. At the same time I am sorry to see how much we Germans are now shut out from studies in most parts of the world.

T. G. HALLE (Stockholm)

The Carboniferous Flora of East Greenland

The known succession of Arctic fossil floras is broken especially by one wide gap, which until lately extended from the top of the Lower Carboniferous to the base of the Upper Triassic. Previous to the Danish Expeditions to East Greenland under Dr. LAUGE KOCH, the post-Devonian Paleozoic floras were thus represented in the Arctic regions only by their oldest phase, that of the Dinantian or Lower Carbonif-

erous in the strictest sense. Of this flora, best known from Spitsbergen, a few species had been recorded (NATHORST 1911) from Hecla Sound in East Greenland; these were then the only Paleozoic plants known from Greenland.

Of the Carboniferous plants collected by Dr. KOCH's early expeditions (HALLE, 1931) some correspond to the Lower Carboniferous ("Kulm") flora of Spitsbergen and of Hecla Sound. But others appeared to represent a higher horizon, chiefly developed in Clavering Island and the western part of Traill Island. The most distinctive forms belonged to the genera *Calamites* (first noted by T. HARRIS) and *Cordaite*s, neither known from Spitsbergen.

The collections made by the later expeditions, up to and including 1938, are still being studied. They contain several other forms which also indicate a post-Dinantian age. Among them are *Sphenopteris adiantoides*, stem-impressions with typical *Heterangium* sculpture, *Sphenopteris fragilis* (in the sense of KIDSTON) and axes with the characteristic lyginodendroid ("Dictyoxylon") sculpture. This little flora, chiefly from Gauss Peninsula, conforms particularly closely to that of the Carboniferous Limestone Series of Scotland. According to the stratigraphical scheme adopted by the Heerlen Conference, it should be classified as lower Namurian, that is, lowermost Upper Carboniferous.

A few fragments, especially a poorly preserved *Alethopteris*, may indicate that the plant-bearing series of Traill Island continues up into the lower Westphalian.

The most surprising discovery, however, was made on the north coast of North Scoresby Land. In a thick series of black shales were collected a few species, particularly a conifer of the *Walchia* type (*Lebachia parvifolia* FLORIN) and *Calamites gigas*. These two species prove that the beds belong to either the uppermost Upper Carboniferous (Stephanian) or the Lower Permian. A more exact determination of the age is not possible, as both species cross the paleobotanically little marked Carboniferous-Permian boundary. These Permo-Carboniferous

plants represent the only reliable information that we have on the flora and vegetation of the Arctic regions during a period elsewhere marked by great paleogeographical changes.

Thanks to the Danish explorations in East Greenland the greatest gap in the history of the Arctic floras has thus been considerably reduced. The collections that the 1949-50 expedition is expected to bring back will no doubt yield additional information.

Discussion

W. GOTHAN: Es ist sehr erfreulich, dass man jetzt auch oberkarbonische Flora aus dem Gebiet von Ost-Grönland kennt, wenn auch ihr Alter nicht genau festgestellt werden kann. Die Paläobotaniker müssen bei Erwähnung eines namurischen Alters immer daran denken, dass das Namur paläobotanisch gesehen uneinheitlich ist, indem im Namur B und C die mehr oder weniger westfälischen Formen (stratigraphisch gesprochen) beginnen, während das Namur A dagegen einen scharf antiquierten Charakter hat und organisch sich der Flora nach an das Unterkarbon anschliesst. D. STUR hat es daher früher mit der Unterkarbon-Flora verbunden und bei ihr die echte Unterkarbon-Flora des Visé von der „oberen Kulm-Flora“ der Waldenburger und Ostrauer Schichten unterschieden. Der bekannte „Florensprung“ GOTHAN's liegt ja über dem Namur A.

J. WALTON: There is a close general resemblance between the succession of floras represented in East Greenland with those in Scotland, particularly those designated Carboniferous Limestone Series and Lower Westphalian. The tapering leaf of *Psymphyllum* type agrees closely in form with specimens of *Psymphyllum delvali* REN. found in Scotland in the Westphalian.

BRITTA LUNDBLAD (Stockholm)

Heterosporous Lycopodiinae in Mesozoic Floras

Recent studies of megaspores indicate that heterosporous Lycopodiinae were well repre-

sented in the Mesozoic. However, indubitable records of plants of the *Selaginella* type from deposits of this age are extremely rare, although the group is known to date back to Paleozoic times. Our knowledge of the proportion of herbaceous lycopods to the larger forms of the group in Older Mesozoic floras is still very unsatisfactory. The author presents a *Selaginella* from the Rhaetic of Hyllinge in NW Scania (*Selaginellites Hallei*). The distribution of selaginellas in the Scanian Mine formation as reflected by findings of sterile anisophyllous shoots of the *Lycopodites scanicus* type and by megaspores is also discussed. A review of the occurrence of related forms in Mesozoic floras is given in this connection.

See LUNDBLAD, B., in Medd. Dansk Geol. Foren., 11 (1948), No. 3, p. 351-363, 1949, and in Kungl. Svenska Vetenskapsakad. Handl., Ser. 4, Vol. 1, No. 8, p. 9-12, 1950. A third paper dealing with material referred to in this contribution will appear in Svensk Bot. Tidskr., 44, No. 3, 1950.

Discussion

J. M. SCHOFF: I was impressed by the detailed information derived from study of the Scanian material by Miss LUNDBLAD. I have been wondering, in fact, on what basis this very excellent material is distinguished from *Selaginella*.

BRITTA LUNDBLAD: In the present state of our knowledge of Mesozoic floras, I think it is slightly better to reserve the name *Selaginellites* for plant remains of this kind. We have a parallel case in *Equisetites*, i.e. *E. Münsteri*. Certain forms might be included in the living genus, but it would be difficult to distinguish them from others, less completely known.

T. M. HARRIS: The question whether partly known Mesozoic plants are to be included in *Selaginella* or *Selaginellites* is not very important. I congratulate Miss LUNDBLAD on advancing our knowledge of one of the many species known previously from isolated spores only.

J. WALTON: I wish to point out that as no

ligule has been shown to be present and heterophyllously occurs also in *Lycopodium* it is advisable to use the name *Selaginellites* in the case in question. It is not yet certain that any fossil forms of the heterosporous *Lycopodiales* were ligulate.

H. HAMSHAW THOMAS: MISS LUNDBLAD is to be congratulated on her work, which is an interesting and important contribution to our knowledge of Mesozoic plants. It seems probable that plants of the *Selaginella* type were of frequent occurrence in Mesozoic floras. The plant from the Jurassic rocks of the Yorkshire coast in England, which has long been known under the name of *Lycopodites falcatus*, seems to be of this kind, for it has proved to be heterophyllous although no cones containing spores have yet been found.

P. GUTHÖRL (Saarbrücken)

Corynepteriden und ähnliche Gewächse aus dem Saar-Karbon

Die unter den Namen *Alloiopteris* und *Corynepteris* beschriebenen Karbon-Farne gehören zu einer Pflanzen-Familie, der *Zygopteroidae*, die in jeglicher Hinsicht bestens bekannt ist. Wie bereits GOTHAN schon bemerkte, ist sie auch eine der interessantesten fossilen Pflanzen-Gruppen. Ein besonderes Charakteristikum der *Zygopteroidae* besteht darin, dass sich die Wedel an der Basis gabelten, was auch neuerdings Frl. Prof. LECLEROQ an Stücken von *Rhacophyton zygopteroides* aus dem oberen Devon Belgiens wieder festgestellt hat. Mit der Beschreibung einer Anzahl als Abdrücke erhaltener Formen befassten sich besonders GOTHAN (Ruhr- und Oberschlesisches Gebiet), KIDSTON (England) und NĚMEJC (Böhmen), während BERTRAND sich mit strukturbildenden Resten dieser Gruppe befasste.

Im Laufe der Jahre ist es mir gelungen, ein umfangreiches Material an *Corynepteriden* und ähnlichen Gewächsen aus dem Saar-Karbon zusammenzutragen. Mit dessen Untersuchung, Abbildung und Beschreibung habe ich bereits begonnen. Diese Ausführungen sollen als eine

vorläufige Mitteilung aufgefasst werden, da die Untersuchungen noch eine gewisse Zeit beanspruchen werden. Doch soll jetzt schon gesagt sein, dass sich die karbonischen *Corynepteriden* und ähnliche Gewächse in etwa 5 Formenkreise aufteilen lassen:

- I. *Corynepteris cristata*, *saraepontana* u. *essinghi*
- II. *Corynepteris grypophylla*, *coralloides*, *quercifolia* u. *pecopteroides*
- III. *Corynepteris herbstiana*, *tenuissima*, *magnifica* u. cf. *magnifica*
- IV. *Corynepteris angustissima*, *junghani*, *radstockensis*, *similis*, *bifurcata*, *thinfieldioides* u. *erosa*
- V. *Desmopteris connata*, *longifolia* u. *gracilis*.

Hierzu ist noch zu bemerken, dass *Corynepteris pecopteroides* kaum zerschlitzte F. l. O. hat und daher zwischen dem II. und III. Formenkreis den Übergang darstellen dürfte. Im IV. Formenkreis sind die Arten mit \pm parallelrandigen, fast bandförmigen F. v. O., während im V. Formenkreis die mit echt bandförmigen F. l. O. zusammengefasst werden.

Jeder dieser 5 Formenkreise hat auch seine Vertreter im Saar-Karbon:

- I. *Corynepteris cristata*, *saraepontana* u. *essinghi*
- II. *Corynepteris grypophylla*
- III. *Corynepteris* cf. *magnifica*
- IV. *Corynepteris angustissima*, *bifurcata*, *thinfieldioides* u. *erosa*
- V. *Desmopteris longifolia* u. *gracilis*.

Während *Corynepteris essinghi* auch fertil bekannt ist, liegen von *C. cristata* und *saraepontana* nur sterile Reste vor. Von *C. grypophylla*, die oft mit *C. coralloides* zusammengebracht wurde, sind nur wenige sterile Reste bekannt. Sie lässt sich von *C. coralloides* ziemlich gut unterscheiden. *C. cf. magnifica* nimmt offenbar eine Mittelstellung zwischen *C. herbstiana* und der oberschlesischen *C. magnifica* ein. Die noch nicht beschriebene Form *C. bifurcata*, die zum Teil auch fertil erhalten ist, hat etwas Ähnlichkeit mit *C. similis*, wie sie NĚMEJC aus

dem böhmischen Karbon beschrieben hat. *C. thinnefeldioides* hat J. SCHUSTER als *Odontopteris* bezeichnet. Das mir vorliegende Urstück zeigt sehr schön die Wedelgabelung an der Basis. Manche Anzeichen sprechen dafür, auch *Desmopteris longifolia* und vielleicht auch *D. gracilis* in die Gruppe der Corynepteriden einzubeziehen.

Aus anderen Karbon-Gebieten sind noch eine Reihe anderer Arten bekannt, die jedoch hier nicht berücksichtigt werden sollen. Meist sind es Formen, die Einzelfunde darstellen.

Eine grössere Anzahl von Stücken aus dem Saar-Karbon, wie auch aus anderen Gebieten, lässt die für diese Gruppe bezeichnende Doppelrieffung der verhältnismässig kräftigen und breiten Rachis erkennen. Diese Erscheinung hängt bekanntlich mit der Form des Leitbündel-Querschnittes zusammen. Besonders bezeichnend ist, dass die F. v. oder l. O. mit der Rachis ungefähr einen rechten Winkel bilden, was aber durchaus nicht immer der Fall zu sein braucht. Manche Formen, wie *C. essinghi*, *grypophylla*, *coralloides*, *angustissima* und *similis*, besitzen an der Wedelbasis im katadromen Winkel fein zerteilte Aphlebien. Es ist aber auch möglich, dass diese bei weiteren Formen ebenfalls noch nachgewiesen werden können.

Über das Allgemeine der Eptapteridaceen als Unter-Familie der Zygopteriden, in der die Corynepteriden zusammengefasst sind, hat zuletzt GOTHAN (1935) ausführlich berichtet, so dass es sich erübrigt, hier näher darauf einzugehen.

Was die stratigraphische Verbreitung der aus dem Saar-Karbon bekannten, bzw. vorliegenden Formen betrifft, sei folgendes bemerkt. *Corynepteris cristata* ist für das Westfal D bezeichnend. *C. saraeponiana* und *essinghi* kommen im Westfal C und D vor. *C. grypophylla* ist selten und auf den untersten Teil des Westfal D beschränkt. *C. cf. magnifica*, *angustissima* und *thinnefeldioides* sind bis jetzt nur im Westfal C und *C. erosa* nur im Stefan A nachgewiesen. *Desmopteris gracilis* ist aus dem Westfal C und dem oberen Westfal D, *D. longifolia* vorwiegend aus dem Westfal C bekannt.

Besonders verbreitete Formen, sowohl vertikal als auch horizontal, in den europäischen Kohlenbecken sind *Corynepteris essinghi*, *coralloides* und *angustissima*. Die Hauptverbreitung, bzw. den Höhepunkt ihrer Entwicklung hatten die Corynepteriden im Westfal. *C. essinghi*, *quercifolia*, *angustissima* und einige andere Formen, welche letztere aber bald wieder verschwanden, treten bereits im Namur auf. Mit *C. erosa* ist die Gruppe der Corynepteriden im Stefan erloschen. Aus dem nordamerikanischen Karbon sind *C. coralloides* und *angustissima* im Westfal nachgewiesen.

P. GUTHÖRL (Saarbrücken)

Neue Pflanzen-Funde aus dem Karbon und Perm des Saar-Nahe-Gebiets

Im Saar-Nahe- und Pfalz-Gebiet sind die Karbon-Stufen Westfal C u. D, Stefan A, B u. C, sowie das untere Perm (Rotliegendes) lückenlos vorhanden. Während meiner 30-jährigen geologisch-paläontologischen Tätigkeit in diesem Gebiet gelang es mir, nicht nur die Leitfossilien der einzelnen Stufen und Schichten festzustellen und gute Beleg-Exemplare bei meinen stratigraphischen Untersuchungen, grösstenteils in den Gruben unter Tage, immer wieder zu finden, sondern auch eine grosse Anzahl Pflanzen-Formen von paläobotanisch-systematischer Bedeutung zutage zu fördern.

Von Lycopoditen sind zu nennen: *Lepidodendron ophiurus*, *Lepidophloios macrolepidotus* als flachgedrückte Stammreste bis 1,30 m Höhe und 0,70 m Breite, *Pinakodendron*, *Bothrodendron*, *Ulodendron*, *Phialophloios*, *Omphalophloios* und einige neue Formen. Ausserdem liegen eine grössere Anzahl von entsprechenden fruktifizierenden Organresten, Zweigen und Blättern vor. Dasselbe trifft auch für die Sigillarien zu, unter denen sich ebenfalls seltene und bis jetzt unbekannte Formen befinden. Die Articulaten sind reichlich und artenreich vertreten, auch bezüglich der Beblätterung und Fruktifikationen. Die Sphenophyllaceen werden repräsen-

tiert durch *Sphenophyllum myriophyllum*, *cuneifolium*, *majus*, *emarginatum* und *oblongifolium*. Ausser diesen bereits bekannten wurde eine neue Form als Leitfossil festgestellt. Bei *S. myriophyllum*, das im Saar-Karbon in einem bestimmten Schichten-Abschnitt recht häufig vorkommt, konnte ich auf Anregung von Prof. GÖTHAN die von einigen Autoren angenommene und bildlich dargestellte Doppelteilung der pfriemenförmigen Blättchen bis jetzt nicht feststellen. An allen Stücken kann ich nur die einfache Gabelung jeweils an der Basis beobachten.

Sehr umfangreich ist das vorhandene Material an Farnresten. Um einige zu nennen, die auch in fertilen Exemplaren vorliegen, seien *Oligocarpia*, *Crossothea*, *Zeilleria*, *Hymenotheca*, *Asterotheca*, *Acitheca*, *Ptychocarpus*, *Diplazites*, *Corynepteris*, *Renaultia*, *Discopteris*, *Danaeites* und *Senftenbergia* angeführt. Ganz besondere Erwähnung verdienen die recht guten Funde von *Sauropteris guthoerli* HIRMER und *Saurodiscites guthoerli* HIRMER, die sicher zusammen gehören, die erstere steril, die andere fertil, aus dem Westfal C. *Noeggerathia foliosa* wurde erstmalig unter Tage auf primärer Lagerstätte gefunden, sodass man sie jetzt auch stratigraphisch einordnen kann und zwar in die Rothell-Schichten des Westfal C.

Von *Rhacopteris asplenites* habe ich Wedelteile von fast 1 Meter Länge gefunden. Sphenopteriden und Eu-Pecopteriden sind unter den Neufunden reichlich und in vielen verschiedenen Formen vertreten. Dabei stellte sich aufgrund eines zweifach-gefiederten Fundstücks heraus, dass „*Mariopteris*“ SARANA HUTH eine *Sphenopteris* ist. Von Palmatopteriden sind vorhanden: *Palmatopteris geniculata*, *alata*, *furcata*, *spinosa* und eine grössere, neue Form, die leiten den Charakter hat. *Dicksonites* liegt ausser der im Westfal D und Stefan A häufigen *D. pluckenetii* in mindestens zwei neuen Formen vor, von denen eine ebenfalls als Leitform anzusprechen ist. An Neuropteriden wurden eine Anzahl neuer Formen, zum Teil in recht guten Stücken, gefunden. Auch von diesen gilt mindestens eine als Leitfossil. Eine recht eigenartige Form, die mit „*Pecopteris cf. grandifolia*“ (FONT. &

WHITE) ZEILLER Ähnlichkeit hat, stammt aus dem Stefan A. Hierbei ist zu bemerken, dass Neuropteriden im Stefan des Saar-Karbons als allergrösste Seltenheiten gelten. Von Alethopteriden wurden in den letzten Jahren besonders gut erhaltene Exemplare gefunden, wie *A. serli*, *grandini*, *costei* u. a. *Lonchopteridium* wurde sowohl im Westfal C, wie auch im Westfal D in verschiedenen Horizonten gefunden. Auch einige besonders bemerkenswerte Odontopteriden, darunter *O. barroisi* P. B., sind in dem Fundmaterial enthalten. *Potoniea*-Reste liegen von *Neuropteris gigantea* und *Linopteris neuropteroides* vor. *Linopteris obliqua* ist sehr häufig im Westfal D und auf dieses beschränkt. Stammreste von Farnen und Aphlebien wurden in einer Anzahl von Formen und zum Teil beträchtlicher Grösse geborgen. Besonders umfangreiches Pflanzen-Material konnte ich in den letzten 15 Jahren im Stefan C sammeln, da zwei kleine Gruben das in diesem liegende Grenzkohlenflöz zeitweise abbauten.

Wie ich bereits in einer früheren Abhandlung (1940) dargestellt habe, ist *Rhacopteris busseana* für das Westfal C und *Rh. asplenites* für das Westfal D des Saar-Karbons bezeichnend. Neuere Funde haben dies bestätigt; und es trifft auch für die gleichen Funde aus dem böhmischen Karbon zu.

Für das Stefan B konnte der erste Fund eines *Lebachia*-Restes nachgewiesen werden.

An dieser Stelle sei auch wieder betont, worauf auch bereits andere Paläobotaniker, die speziell in Karbon-Gebieten tätig sind, hingewiesen haben, dass die genaue Kenntnis der Karbon-Flora für die Karbon-Stratigraphie und letzten Endes für den praktischen Steinkohlen-Bergbau eine sehr grosse Bedeutung hat. Immer wieder finde ich dies beim Aufschliessen neuer Grubenfelder, bzw. Feldesteile, sei es durch Schächte oder Querschläge und sonstige Ausrichtungsarbeiten, bestätigt. Besonders erfolgreich waren die entsprechenden Untersuchungen von Tiefbohrungen, die in den letzten Jahren im saar-lothringischen Gebiet niedergebracht wurden. In besonderen stratigraphischen Tabellen ist die vertikale Verbreitung

der hauptsächlichsten Pflanzenarten (Leitfossilien) unter Berücksichtigung eines bestimmten Maßstabs für die Schichten-Mächtigkeiten und der petrographischen Leit-Horizonte, eingetragen. Diese liegen im saar-lothringischen Karbon in Form von schwächeren oder stärkeren Tonsteinbänken vor.

Bei dieser Gelegenheit sollen die Paläobotaniker anderer Kohlen-Revire angeregt werden, bei ihren eventuellen stratigraphischen Arbeiten und Untersuchungen auf das Vorkommen von Tonsteinen besonders zu achten. Nach meinen bisherigen Erfahrungen und Feststellungen ist ihr unmittelbares Liegendes immer kohlige Substanz, entweder Kohle, unreine Kohle oder Brandschiefer. Dagegen kann das unmittelbare Hangende der Tonsteine ausser kohligler Substanz auch Sandstein, Sandschiefer oder Schiefertone sein. Sind die Tonsteine einmal gefunden, so stellen sie meist markante Leit-Horizonte dar, da sie in horizontaler Richtung auf weiter Erstreckung aushalten. Bis jetzt sind Tonsteine aus folgenden Karbon-Gebieten bekannt: Saar-Lothringen, Mittel-Frankreich, Schottland, Ruhrgebiet, Sachsen, Oberschlesien, Niederschlesien und Böhmen.

Besonders interessieren dürfte, dass in den letzten 3 Jahren in den Waderner Schichten des oberen Rotliegenden bei Sobernheim an der Nahe in sandigen Schiefen und sehr feinkörnigen Schiefertönen ein umfangreicher Pflanzen-Verein nachgewiesen wurde. Ausser mir haben dort besonders erfolgreich gesammelt die Herren Dr. K. W. GIEB vom Geologischen Institut der Universität Mainz und O. ERMANN aus Sobernheim. Sehr häufig sind hier *Astrotheca arborescens*, *Dicksonites*, *Neuropteris cordata-ovata* und *Calamites gigas* vertreten. Als Einzelfunde, aber in grossen und gut erhaltenen Stücken, sind *Lebachia piniiformis* und *Odontopteris subcrenulata* zu nennen. Da aus dem über den Waderner Schichten liegenden obersten Glied des Rotliegenden, den Kreuznacher Schichten, bis jetzt noch keine Pflanzen-Reste nachgewiesen sind, handelt es sich in den beiden eben genannten Formen um die jüngsten bekannten Vorkommen ihrer Art.

Discussion

W. GOTHAN: Obwohl das Saar-Karbon nur die Karbonstufen Westfal C und Westfal D ausser dem Stefan aufzuweisen hat, lässt sich innerhalb der erstgenannten beiden eine ungewöhnlich gute Stratigraphie in diesem Revier durchführen. Das war schon durch frühere Untersuchungen bekannt, aber es ist wesentlich das Verdienst des Vortragenden, dass er durch seine langjährigen intensiven Studien in seinem Heimatrevier eine so weitgehende und vieles Neue bietende Stratigraphie auf Grund der Pflanzen erreicht hat, wie er sie uns vorgeführt hat. So wird allmählich durch seine Arbeiten und die der wieder im Revier arbeitenden französischen Autoren eine Genauigkeit unserer Kenntnisse der dortigen Karbonflora erreicht werden, wie sie in keinem anderen der deutschen oder ehemals deutschen Kohlenreviere zu verzeichnen ist. Wie von mir vorausgesagt, werden trotz unvermeidlicher Subjektivität der Autoren eine Reihe von neuen Arten zum Vorschein kommen, worin er uns bei der Vorführung der *Corynepteriden* ein Beispiel gegeben hat. Auch der Bergbau hat seinen Nutzen davon.

T. KOBAYASHI (Tokyo)

The Transformation of the Permo-Triassic Flora in East Asia Elucidated by the Climatic Change Caused by the Akiyoshi Crustal Deformation

In East Asia there are two distinct Permian floras. One is the Jido type rich in Euramerian Permo-Carboniferous elements, and the other the Kobosan type containing *Gigantopteris nicotianaeifolia*. In Korea the Jido Series yields Sakumarian fusulinids in the lower part, and the upper part is rich in plants. Both the upper Jido and its equivalent formations in South Manchuria and North China are the main coal-bearing strata in which black shale preponderates. The variegated Kobosan and its equivalents contain many layers of alumin-

ous shale; passing upward the rock colour becomes lighter, and coal-measures, though intercalated, become less frequent until coal and plants are totally absent in the Greenstone series. This succession appears to show evidence of climatic change from warm and humid in the late Jido, to arid in the Greenstone period.

The Akiyoshi orogenic cycle which is well exemplified in Japan (Journ. Fac. Sci. Imp. Univ. Tokyo, Sect. 2, Vol. 7, Pt. 7, 1941) is traceable into Tonkin, and a sympathetic movement is recognizable in China. Therefore, it is reasonable to assume that the geanticlinal culmination in the early part of the cycle was responsible for the climatic change in the inland areas embraced by this culminating axis.

From KAWASAKI's monograph on the Heian flora of Korea, and from OISHI's on the Mesozoic flora of Korea and the Japanese islands, it is found that 15 genera and 5 species are common between the Jido and Kobosan floras, while the Mine group of floras (i.e. the *Dictyophyllum* series) has only 6 or 4 genera in common with the Jido and Kobosan flora respectively. The difference is significantly greater within the Mesophyticum than between the Mesophyticum and Palaeophyticum; and further, the Mine is more similar to the Jido than to the Kobosan flora. The retardation of the evolution of floras in East Asia must depend upon the climatic changes caused by the crustal deformation. More precisely, this was the Permo-Carboniferous Variscan orogenic cycle on the western side of Eurasia, and the Permo-Triassic Akiyoshi cycle on the eastern side, where its paroxysm was in the Ladinian-Carnic in Japan and the Noric in Tonkin.

The Mine floral group, which is similar to the Rhaeto-Liassic floras in Scania, Bornholm, Greenland, and elsewhere, occurs as early as the Carnic period in East Asia in the monsoon region along the Akiyoshi orogenic zone, as demonstrated in my paper on the Mesozoic climate in East Asia (Japan. Jour. Geol. Geogr., Vol. 18, 1942). The closer alliance of this flora to the Jido flora than to that of the Kobosan may be a proof that the Jido flora

flourished in a climate si.
Mine.

In the absence of the author's contribution, it is to be noted that the abstract was read by R. FLORIN. *ist zu bemerken, dass des Saar-Karbons als alten. Von Alethopte-*
Callixylon Velinense nov. sp., un Jaren besonders
ture conservée du Dévonien de laden, wie A. serli,

Le bois fossile en partie silicifié (*tyridium* wurde récolte H. MARCELLE) sur lequel est *estfal D* in la diagnose ci-après, provient de l'assise des *ci-*
» Roches rouges de Mazy » à Sart-Dame-
Avelines, assise située à la base du Dévonien
supérieur.

Plante ligneuse, tige atteignant environ 5-7 cm de diamètre; moelle axiale d'environ 1,5 cm de diamètre; bois secondaire à structure de type gymnospermien, formé de trachéides et de rayons.

Coupe transversale: Trachéides de dimensions et de formes irrégulières, d'un diamètre d'environ 10 à 30 μ , à lumina subquadrangulaires radialement elliptiques ou subcirculaires, à membrane épaisse d'environ 7-15 μ ; rayons d'une cellule de largeur.

Coupe radiale: Trachéides à ponctuations disposées en groupes, alignés radialement, et, dans chaque groupe, suivant le type alterne multisérié en 1-3 (2 le plus fréquemment) files verticales; ponctuations aréolées, circulaires-subelliptiques, d'un diamètre de 8-12 μ , à orifices (pori) en forme de fente diagonale, les deux orifices opposés d'une paire de ponctuations offrant en projection l'aspect d'une croix aux branches se coupant à angles variables et longues comme à peu près deux diamètres croisés. Cellules de rayons d'une longueur de 50-170 μ , d'une hauteur de 28-42 μ (en moyenne 30-35 μ). Trachéides de rayons épars ou plus rarement alignés, d'une long. atteignant environ 190-200 μ ; correspondant approximativement au diamètre total de 4-6 trachéides contigus, et d'une hauteur d'environ 30-45 μ , à ponctuations.

Coupe tangentielle: Rayons assez nombreux, 12-15 par 0,5 mm², strictement unisériés; cellules

et trachéides de rayons d'une largeur d'environ 16-28 μ (21-22 μ en moyenne); rayons d'une haut. de 1-13 cellules (le plus souvent 3-4, rarement de plus de 6 cellules); cellules marginales supérieures et inférieures de rayons d'une haut. atteignant 50 μ , à contour ogival ou sub-ogival.

Conclusions: La structure relativement bien conservée de *C. Velinense* nous a permis d'établir avec certitude la présence de ce genre en Belgique.

Remarquons le polymorphisme du genre *Callixylon* et notons certaines tendances morphologiques particulières manifestées, d'une part, par les espèces du groupe oriental (Europe) et, d'autre part, par celles du groupe occidental (Amérique du Nord) de l'aire de dispersion du genre.

Callixylon Velinense est une espèce voisine, mais distincte des autres espèces signalées en Europe; ses rayons sont *strictement* unisériés.

Des espèces occidentales, *C. bristolense*, qui occupe déjà une position systématique particulière en raison de ses punctuations à orifices verticaux, est la seule à avoir des rayons unisériés et, exceptionnellement, des rayons plus larges; cette structure rappelle celle des trois espèces à rayons non strictement unisériés du groupe oriental; les rayons chez les autres espèces occidentales sont plus ou moins fréquemment plurisériés.

Alors que chez plusieurs espèces occidentales les zones d'accroissement sont ébauchées ou nettement marquées, ces zones n'ont pas été signalées chez les espèces du groupe oriental; chez ces dernières, la structure du bois secondaire tendrait à faire admettre l'existence d'un climat tropical au Dévonien supérieur en Europe, tout au moins à 49°-51° Latitude N. Ces

quatre espèces, toutes dévoniennes, présentent, au surplus, pour l'une, l'unisériation stricte et, pour les autres, une tendance très nette à la prédominance de l'unisériation des rayons, ce qui pourrait être un caractère primitif. Chez les deux espèces les plus anciennes (Frasnien), les trachéides ont des punctuations dans les parois radiales, tandis que chez *C. Henkei* (Famennien) les trachéides ont des punctuations dans les parois radiales et les parois tangentielles, les punctuations de celles-ci étant différenciées, ce qui constituerait une progression évolutive, peut-être en rapport avec l'âge plus récent de cette espèce.

C. Trifilievi, enfin, possède des trachéides à punctuations sur les parois radiales et ordinairement sur les bords des parois tangentielles; on pourrait considérer cette forme comme un type morphologique de transition évolutive.

Il est probable et souhaitable que les progrès de l'étude de la systématique du genre *Callixylon* aboutisse à une distinction de sous-genres ou sections de genre (« Uniseriati », « Pauciseriati », « Pluriseriati », etc.) permettant de constituer des groupes naturels d'espèces.

ARNOLD a insisté sur l'abondance des fossiles rapportés à *Callixylon*, trouvés dans certaines « strates » en Amérique du Nord, et a mis en évidence l'importance du genre en question, en tant que type commun de la végétation du Dévonien supérieur. Peut-être y a-t-il lieu d'attendre que l'on ait récolté plus de matériaux en Europe pour étendre à ce continent les intéressantes conclusions d'ARNOLD.

This paper had arrived too late for inclusion in the programme of Session 2. The author herself being absent, an abstract was read by F. STOCKMANS.

PHYTOGEOGRAPHY, PHG

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Recorder: G. E. DU RIETZ

Vice-Recorder: H. SJÖRS

SESSION I

July 12th, 1—4 p. m.

Chairman: C. TROLL, Records: G. E. DU RIETZ and H. SJÖRS

SUBJECT:

Tropical Flora and Vegetation

G. E. DU RIETZ opened the Session, wished the phytogeographers welcome to their work, and asked Professor C. TROLL to read his Presidential Address.

C. TROLL (Bonn)

Presidential Address: Der Vergleich der Tropenvegetation der Alten und Neuen Welt

Der Vergleich der Vegetation zwischen floristisch scharf getrennten Gebieten muss auf das Studium der pflanzlichen Lebensformen und ihrer geographisch-ökologischen Bedingungen gegründet werden. Die Tropenvegetation der Alten und Neuen Welt bietet dafür mannigfaltige Möglichkeiten, wie schon die bekanntesten Beispiele konvergenter Lebensformen erkennen lassen (stammsukkulente Cacteen, Euphorbiaceen und Asclepiadaceen; blattsukkulente Agaven, Aloë, Bromeliaceen und Sansevierien; arborescente Espeletien und Senecionen etc.). Da jede Pflanzenassoziation aus einer bestimmten Auswahl von Lebensformen zusammengesetzt ist und ein sogenanntes Lebensformenspektrum aufweist, ergibt sich weiter die Möglichkeit des Vergleichs ökologisch entsprechender Vegetationsformen mit Hilfe des Lebensformenspektrums.

1. Gliederung der Tropenvegetation

Tropenklimate, auch die Klimate der tropischen Gebirge, sind Klimate ohne deutliche thermische Jahreszeiten. Daher ist man sich darüber einig, dass die klimatischen Vegetationsgürtel der Tropen — abgesehen vom Vertikalprofil — nach dem Grade der Feuchtigkeit gegliedert werden müssen. Nach F. JAEGER (1945) unterscheidet man im Tiefland zweckmässig 6 Gürtel abnehmender Feuchtigkeit: Regenwaldgürtel, Feuchtsavannengürtel, Trockensavannengürtel, Dorn- und Sukkulenten-Savannengürtel, Halbwüstengürtel, Wüstengürtel. Dabei ist das Wort Savannen nicht physiognomisch im Sinne von A. F. W. SCHIMMER zu verstehen, auch nicht als Bezeichnung für eine einzelne Vegetationsformation, sondern als Formationskomplex innerhalb klimatischer Vegetationsgürtel. Denn in allen „trophilen“ Gürteln vom Feuchtsavannengürtel bis zum Dornsavannengürtel sind sowohl reine Grasfluren als geschlossene Wälder als auch von Bäumen und Gehölzen durchsetzte Grasfluren

weit verbreitet. Der Anteil von Gras- oder Holzpflanzen ist in den Tropen kein Ausdruck des Klimas. SCHIMPER hat die seinem Werke zu Grunde gelegte Reihe Wald-Grasland-Wüste irrümlicherweise als eine klimatische Reihe aufgefasst. Das physiognomische Bild der tropischen Savannengürtel ist vielmehr ein Ausdruck edaphischer, biotischer und anthropogener Faktoren. Im Feuchtsavannengürtel treffen wir alle Formen von der baumfreien Grasflur („Campo limpo“) über den „Campo sujo“ bis zum Savannenwald („Campo cerrado“), im Trockensavannengürtel ebenso alle Formen von der baumfreien Trockengrassavanne bis zum geschlossenen Trockenwald (Miombowald und Mopanewald Afrikas, *Piptadenia*- und Tipuanawald Südamerikas), im Dornsavannengürtel alle Formen von der ariden Grasflur bis zum geschlossenen Dorn- und Sukkulente-Wald (Caatinga-Typus). Caatingawälder gehören einer klimatisch viel trockeneren Zone an als Campos.

2. Klimatische Grundlagen der tropischen Vegetationsgürtel

Es gelingt nicht, die Gliederung der klimatischen Vegetationsgürtel mit einer Niederschlagskarte zur Deckung zu bringen. Auch hygrothermische Koeffizienten, die auf Jahresmittel aufgebaut sind, wie der Regenfaktor R. LANGES, der Ariditätsindex DE MARTONNES u. a., sind dafür nicht ausreichend. Einen grossen Schritt weiter führt ein neuer, von meinem Schüler W. LAUER durchgeführter Versuch, die Ariditätsindizes für die einzelnen Monate des Jahres zu berechnen und die Ariditätsdauer nach der Zahl der ariden und humiden Monate in sogenannten „Isohygromenen“ darzustellen. Es ergeben sich aus dem Vergleich der Vegetationskarte und der Isohygromenenkarte Afrikas und Südamerikas folgende Beziehungen:

12	-9 $\frac{1}{2}$	humide Monate Regenwaldgürtel
9 $\frac{1}{2}$	-7	humide Monate Feuchtsavannengürtel
7	-4 $\frac{1}{2}$	humide Monate Trockensavannengürtel
4 $\frac{1}{2}$	-2	humide Monate Dornsavannengürtel
2	-1	humide Monate Halbwüstengürtel
0		humide Monate Wüstengürtel

Die PENCKSche Trockengrenze, dargestellt für Afrika von F. JAEGER, für Südamerika von E. SORGE, liegt bei 6 $\frac{1}{2}$ -7 humiden Monaten, die agronomische Trockengrenze (Grenze des Regenfeldbaues), dargestellt für Afrika von E. R. FALKNER, bei 4 humiden Monaten.

Durch die neue Darstellung wird es erklärlich, warum in Afrika so ausgedehnte Waldgebiete vom Typ der Trockensavannenwälder (Miombo- und Mopanewälder) vorkommen, während in Südamerika die entsprechenden *Piptadenia*- und „Mimosa“-Wälder nur schmale Streifen einnehmen. Denn die Trockenstufen 5-7 humide Monate sind in weiten Gebieten des östlichen und südöstlichen Afrika, aber nur in schmalen Übergangszonen in Südamerika vertreten. Abweichungen in Einzelfällen bleiben bestehen, z. B. Regenwälder an der Guinea-Küste schon bei 9 humiden Monaten wegen besonders hoher Niederschlagsmengen in der Regenzeit, Dornsavannen in Nordostbrasilien noch bei 5-6 humiden Monaten wegen aperiodischer Dürrejahre.

3. Lebensformen der tropischen Klimagürtel

Die Lebensformen des Regenwaldes sind hinreichend bekannt und oft beschrieben, die der Savannengürtel dagegen noch sehr unvollkommen klassifiziert. Ausschlaggebend sind auch für die tropischen Tropophytengürtel die Lebensformen der Bäume, da die baumfreien Formationen natürliche oder künstliche Ausleseformen darstellen.

Die auffallenden Konvergenzen alt- und neuweltlicher Lebensformen der Tropen gehen nach meinen Erfahrungen in Südamerika und Afrika besonders auf vier Erscheinungen zurück: die Form der Blätter, den Grad der Bedornung, die Art der Berindung und die Wasserspeicherung.

a) Im Feuchtsavannengürtel treten, wenn die fehlende klimatische Feuchtigkeit durch Bodenfeuchtigkeit ersetzt wird, noch allgemein immergrüne, hygrophile Gehölze auf, z. B. immergrüne Uferwälder (Riverine Forests, Fringing Forests), Schluchtwälder, Termitengehölze. Die Bäume der trockenen Standorte

sind im allgemeinen mit rauen, rissigen Rinden, mit dicker Korkschicht ausgezeichnet. Ihr Laub ist vorwiegend gross und ganz-randig oder breitfiedrig (Bauhiniin-Typ). Sie zeigen keine sichtbaren Zeichen der Wasserspeicherung, da die meisten Holzgewächse auch in der Trockenzeit das Grundwasser erreichen. Nur Pflanzen von geringem Tiefgang der Wurzeln haben Xylopodien (F. RAWITSCHER). Grasbrand ist weit verbreitet und die Grassavannen können als „Fire-Climax“ aufgefasst werden.

b) Im Trockensavannengürtel treten die immergrün-hygrophilen Waldinseln und Uferwälder allmählich zurück. Die grössere Trockenheit macht sich bemerkbar in dem Vorherrschen des mittelfiedrigen (*Berlinia*-Typ) oder kleineren, ganzrandigen Laubes (*Combretum*-Typ). Die Rinden zeigen noch dicke Borken (wohl eine Auslese durch den Grasbrand), die ziemlich dichte Grasdecke erlaubt noch das regelmässige Brennen, auch unter dem lichten Dach des geschlossenen Trockenwaldes.

c) Im Dornsavannengürtel mit den Dornwäldern erzeugt das aride Klima besonders markante Anpassungsformen: 1. Grüne, assimilierende Rinden mit papierartiger Borke, die teils in grossen Fetzen, teils in kleinen Schuppen abgestossen werden und die Baumstämme entweder grün oder weisslich erscheinen lassen. Die assimilierenden Rinden sind offensichtlich ein Ersatz für die lange Zeit der Entlaubung. 2. Bedornung der meisten baum- und buschförmigen Holzgewächse und der Stammsukkulanten. 3. Das Vorherrschen des Feinfiederlaubes vom Akazientypus. 4. Die Wasserspeicherung in Form von Stammsukkulanten, Blattsukkulanten, Wasserhölzern und Flaschenbäumen (z. B. *Adansonia*, *Ceiba*, *Cochlospermum*, *Carica*, *Pachycormus*, *Pachypodium*, *Adenium*, *Didiera*, *Cotyledon* u. a.) und unterirdischen Xylopodien. Ufer- und Grundwasserwälder sind mit Vorliebe von Fächerpalmen (*Copernicia* in Amerika, *Hyphaene* in Afrika) gebildet.

d) Wüstensteppen sind Verarmungs- und

Reduktionsformen der Dornsavannen durch Ausfall der Bäume oder ihre Verkümmern zur Strauchform und durch das Zurücktreten der ausdauernden Kräuter und Gräser, im übrigen aber in den Lebensformen den Dornsavannen ähnlich.

4. Höhenstufen

Die bekannten 4 klimatischen Höhenstufen des tropischen Amerika *Tierra caliente*, *T. templada*, *T. fria* und *T. helada* werden im immerfeuchten Bereich durch die folgenden Vegetationsstufen vertreten: Tropischen Tieflands-Regenwald (Tropical Lowland Evergreen Rain Forest), tropischen Bergwald (Tropical Lower Montane Forest), tropischen Höhen- und Nebelwald (Tropical Upper Montane Forest) und die Páramo-Vegetation. Besonders charakteristisch sind in allen feuchten Tropengebirgen die Lebensformen des Höhenwaldes (Anden, Mittelamerika, Ostafrika, Südindien und Ceylon, Sunda, Ozeanien). Schon in mittleren Höhen treten meist Baumfarne und Bambuseen auf, der Epiphytismus (Farne, besonders auch Hymenophyllaceen, Moose, Flechten, Orchideen, Bromelien etc.) steigert sich mit der zunehmenden Luftfeuchtigkeit nach der Höhe zu. Die seltsamste Konvergenz der Lebensformen zwischen Kryptogamen und Phanerogamen stellen *Usnea barbata* und die neuweltliche *Tillandsia usneoides* dar. An der Waldgrenze bilden die lorbeerblättrigen Bäume (vom Typus *Weinmannia*, *Clethra*, *Myrica*, *Rapanea*, *Podocarpus*) Schirmkronen mit gewölbter Oberfläche und einer nur sehr dünnen oberflächlichen Belaubung („immergrüne Kugelschirmbäume“). Eine weitere, ökologisch noch ungeklärte Eigenart der Pflanzen des Höhenwaldes sowohl der Alten als der Neuen Welt ist das starke Hervortreten rost- bis zimtbrauner Behaarung von Sprossen, Blattstielen und Blattunterseiten. Wo nicht eine mit der Höhe wiederabnehmende Feuchtigkeit dem Walde nach oben eine frühere Grenze setzt, dürfte seine Höhengrenze mit der Häufigkeit der Frostwechsel in Zusammenhang stehen.

Entsprechend den immerfeuchten Höhengür-

tein müssen auch die höheren Stufen der trockeneren Bereiche unterschieden und nach ihren Lebensformen charakterisiert werden. Wie im Tiefland Regenwald und Feuchtsavanne, so kann man in der Höhenstufe der Tierra templada allenthalben in den Tropen, in Brasilien, West- und Ostafrika und in Indien, feuchten Berg- und Höhenwald (Montane Forest) und Höhengrasland oder Höhensavanne (Montane Grassland) ausscheiden und wieder in feuchte und trockene Höhensavanne differenzieren. Die trockeneren Klimabereiche der grösseren Höhen kommen innerhalb der Tropen allerdings nur im Bereiche der Kordilleren Amerikas vor, wo in der Puna de Atacama sogar die Wüste bis in die höchsten Höhen aufsteigt. Nur dort können wir daher auch ein vollständiges System aller möglichen Höhen- und Feuchtigkeitsbereiche verifiziert finden. Innerhalb der Hochgebirgsstufe (Tierra helada)

zwischen der Wald- oder Ackerbaugrenze einerseits und der Schneegrenze andererseits sind Gürtel verschiedener Feuchtigkeitsgrade ähnlich wie im Tiefland entwickelt. Nach früheren Vorschlägen des Verfassers können wir dort (um eine Stufe vermehrt) gliedern in: Paramo — feuchte Puna — Trockenpuna — Dorn- und Sukkulenten-Puna und Wüstenpuna. Für die Vegetation mittlerer Höhenlagen schlage ich, zusammen mit W. LAUER, vor, die Landschaftsbezeichnungen „Sierra“ für die Täler und Gebirgshänge der kühlen Stufe (Tierra fria) und „Valle“ für die Täler und Hänge der Tierra templada-Stufe zu gebrauchen, und dann weiter nach dem Grade der Feuchtigkeit zwischen feuchter, trockener und Dorn-Valle-Vegetation (Wald und Grasland) und zwischen feuchtem, trockenem und Dorn-Sierra-Busch zu unterscheiden, wie es in der Tabelle geschehen ist.

Horizontal and Vertical Arrangement of Climates and Climatic Vegetation Types in the Tropical Andes

Number of Humid Months (accord.to W. LAUER)	Tierra Caliente Lowland	Tierra Templada Lower Montane Stage	Tierra Fria Upper Montane Stage	Tierra Helada High Montane Stage
12	Tropical Lowland Evergreen Rain Forest	Tropical Lower Montane Forest	Tropical Upper Montane Forest	Paramo
11	and			
10	Tropical Lowland Semievergreen Rain Forest			
9	Tropical Moist Decid- uous Forest and	Tropical Moist	Tropical Moist	Moist Puna
8	Grassland	Valle-Vegetation (Forest and Grassland)	Sierra-Vegetation (Moist Sierra Bush)	(Shrub and Grassland)
7				
6	Tropical Dry Decid- uous Forest and	Tropical Dry	Tropical Dry	Dry Puna
5	Grassland	Valle-Vegetation (Forest and Grassland)	Sierra-Vegetation (Dry Sierra Bush)	(Shrub and Grassland)
4				
3	Tropical Thorn Forest and Grassland	Tropical Thorn	Tropical Thorn	Thorn Puna
2		Valle-Vegetation (Forest and Grassland)	Sierra-Vegetation (Thorn Sierra Bush)	(Shrub and Grassland)
1	Tropical Desert Shrub	Tropical Valle-Desert Shrub	Desert Sierra	Desert Puna
0	Tropical Desert	Tropical Valle-Desert		

Discussion

G. E. DU RIETZ: I wonder whether it would be possible to extend the parallelisation of tropical vegetation types demonstrated by our President also to the tropical vegetation of Australia, where deciduous trees are insignificant owing to the dominance of evergreen taxonomic units as *Eucalyptus* and phyllodian *Acacia* from very wet to very dry climates. An extension to tropical Australia of Prof. TROLL's parallelization may prove useful for phytogeography.

W. ROBYNS and C. TROLL also took part in the discussion.

P. W. RICHARDS (Bangor)

The Structure of Tropical Evergreen Forest in America, Asia and Africa

The primary Tropical Rain Forest of the Old and New Worlds consists of communities of two kinds: Mixed Forest associations (with numerous dominants) and Single-dominant communities. The latter, which may be regarded as consociations or societies, according to their extent and importance, are usually found on special soil types and seem to depend on non-optimal soil conditions.

The Mixed Forest associations found in tropical America, Asia and Africa respectively have a fundamentally similar plan of structure, as was demonstrated by means of profile diagrams showing the stratification. The number of tree stories appears always to be three and these may be termed the A, B and C stories.

The structure of Single-dominant forests has been little investigated, but in some cases at least they have only two well-defined tree stories, e.g. the *Eperua falcata* consociation of British Guiana has an AC structure, different from the ABC structure of the Guiana Mixed Forest.

In conclusion it was shown that special

edaphic types of rain forest, e.g. those found on Lowland Tropical Podzols in Borneo and British Guiana, may be strikingly similar in structure in widely separated tropical regions, though of course floristically quite unlike.¹

Discussion

J. LANJOUW: Which are the special soil conditions that are responsible for the tropical forest with dominant species and for the mixed forest?

A. S. THOMAS suggested that the two different types of tropical evergreen forest could be explained best by the theory, for which there is increasing evidence, that the mixed forests are not true climax forests, but that the forests with one dominant species, such as *Mora excelsa* in Trinidad and *Cynometra alexandri* in East Africa, are true climax forests. Just as in temperate regions, there are often few species in climax vegetation of tropical regions.

P. W. RICHARDS: 1. To Professor J. LANJOUW. The available evidence suggests that mixed tropical evergreen forests tend to occur where the soil conditions are optimal and forests with single dominant species where the soil is in some way or another relatively unfavourable, e.g. water-logged, very shallow or (as on tropical podzols) excessively leached and mineral-deficient. 2. To Dr. A. S. THOMAS. I know that in some places, e.g. Budongo in Uganda, according to EGGELENG, there seems to be a succession from mixed to single dominant forest, but I do not agree that mixed forests are necessarily not true climaxes. In my opinion, as I said in reply to Professor LANJOUW, single dominant forests are usually climaxes only under special soil conditions.

C. TROLL and W. ROBYNS also took part in the discussion.

¹ For further information see: P. W. RICHARDS, *The Tropical Rain Forest. An Ecological Study*. Cambridge 1952.

W. ROBYNS (Bruxelles)

On the Phytogeographic Elements in the Congo Flora

The term element has been used in the literature in a wide variety of applications so that it is necessary to distinguish its different meanings by definite adjectives. We use here the term as a purely geographical concept, that is, indicating taxa with similar phytogeographical areas.

Owing to its geographical situation in the heart of tropical Africa, Congo has a Flora with a great variety of phytogeographical elements. Their exact definition is still difficult on account of the actual imperfect state of our taxonomic knowledge of the Congo Flora and of the Tropical African Flora in general. Therefore we intend only to give a survey of the most important distribution types of the Flora of Belgian Congo and Ruanda-Urundi, based on the "Flore du Congo Belge et du Ruanda-Urundi, Spermatophytes I (1948), II (1950)."

Besides widespread elements of minor phytogeographical importance (cosmopolitan, pan-tropical, paleotropical and neotropical) and several linking elements (afro-malagasian, afro-austroafrican, afro-mediterranean and afro-macaronesian), we have mainly to deal with the African elements which form the basic group of the Congo Flora. They can mainly be classified as follows:

1. *Panafrican elements*, distributed all over tropical Africa: *Ficus Vallis-Choudae* Del.

2. *African elements* of limited distribution in Tropical Africa:

a) Tropical Africa without West Africa: *Ficus capraefolia* Del.

b) West, East and North-East Africa: *Ficus Hochstetteri* (Miq.) A. Rich.

c) North-East, East and South-tropical Africa: *Oxygonum sinuatum* (Hochst. et Steud.) Benth. et Hook.

d) North-tropical, East and South-tropical Africa: *Clematis Oliveri* Hutch.

e) West and East Africa: *Chaetacme microcarpa* Rendle.

f) West and South-tropical Africa: *Ficus Nekbudu* Warb.

g) West and North-tropical Africa: *Nymphaea maculata* Schum. et Thonn.

h) North-East and East Africa: *Loranthus curviflorus* Benth. et Oliv.

i) East and South-tropical Africa: *Aristolochia persiana* Klotzsch.

j) Endemic elements distributed in several phytogeographical districts: *Ficus amadiensis* De Wild., *Thesium Wittei* De Wild., *Loranthus ituriensis* De Wild.

3. *Guinean elements* of three types:

a) Guinean: *Piper guineense* Schumach. et Thonn.

b) Congo: *Gnetum africanum* Welw.

c) Endemic: *Peperomia dubia* Balle, *Ficus kimuensis* Warb., *Dorstenia Laurentii* De Wild., *Encephalartos Poggei* Aschers.

4. *Oriental elements* of three types:

a) oriental: *Viscum Hildebrandtii* Engl.

b) Central-African: *Dorstenia Brownii* Rendle.

c) endemic: *Ficus ruwenzoriensis* De Wild., *Kalanchoe bentensis* De Wild.

5. *Zambezian elements* of three types:

a) Zambezian: *Clematis Welwitschii* Hiern.

b) Bangwelo-Katanga: *Dorstenia Debeersii* De Wild. et Th. Dur.

c) endemic: *Dorstenia Homblei* De Wild.

6. *Sudanese elements*: *Encephalartos septentrionalis* Schweinf.

7. *Ethiopian elements*: *Girardinia bullosa* (Hochst.) Wedd.

In eastern Congo and Ruanda-Urundi, there are various types of mountain species. They have mostly discontinuous areas: *Podocarpus milanjanus* Rendle, *Ranunculus extensus* (Hook. f.) Schube, *Ocotea usambarensis* Engl., but some endemic species are limited to one single mountain: *Sedum churchillianum* Robyns et Boutique (Western Ruwenzori), *Pilea kiwuensis* Engl. (Sabinyo).

OLOV HEDBERG (Uppsala)
*Vegetation Belts of the East African
Mountains*

East Africa consists largely of more or less undulating highlands with an altitude between 800 and 2000 m. Its vegetation is mostly formed by different types of savanna and steppe. Over these uplands arise, like islands in a sea, a number of isolated mountains, some of which attain heights between 4000 and 6000 m. Their higher parts harbour a vegetation which differs very much from the surrounding savanna. The interesting floras of these mountains have been studied by several botanists, and so have their vegetation regions, but earlier no comparative study seems to have been made of the vegetation belts of all the mountains. In 1948, the present author had the opportunity to visit seven of the highest ones, viz. Ruwenzori, Muhavura, Mt Elgon, Aberdare, Mt Kenya, Kilimanjaro and Meru. On the basis of observations then made and of literature available, the following survey was compiled.

There are three significant vegetational limits, which recur on all the mountains investigated, namely (1) the lower limit of the mountain rain forest towards the savanna or steppe, (2) the upper limit of the mountain forest towards the Ericaceous vegetation, and (3) the upper limit of the continuous Ericaceous vegetation.—We may, accordingly, distinguish three main vegetation belts on the mountains: (I) the (montane) forest belt, (II) the (subalpine) Ericaceous belt, and (III) the alpine belt.

The montane forest belt usually extends from c. 1700–2300 m to c. 3000–3200 m. On some mountains it can be subdivided into three different zones, viz. (1) the mountain rain forest zone, (2) the bamboo zone, and (3) the *Hagenia-Hypericum*-zone, as on Mt Kenya, Aberdare, and some of the Virunga volcanoes. Elsewhere the third zone may be missing, as on Elgon and Ruwenzori, or both bamboo- and *Hagenia-Hypericum*-zones are

wanting, as on Kilimanjaro and the northern half of Meru. On the western side of Meru, *Hagenia* seems to be the dominant forest tree throughout the belt.

The Ericaceous belt is dominated by arborescent or shrubby species of *Philippia* and *Erica*. This belt, which usually occurs between 2600–3300 and 3550–4000 m, has a very different character on different mountains. Thus on Ruwenzori it is represented by a dense and moist forest zone with 7–8 m high *Philippia* and *Erica* trees, and on Kilimanjaro by a dry Ericaceous shrub-zone with 1/2–1 m high shrubs of the same genera. On Elgon and Kilimanjaro the lower part of the belt consists of a "moorland" zone with dominant tussock-grasses and sparse trees or shrubs of *Philippia* and *Erica*. The vast moorlands of Aberdare, however, seem to correspond to the upper part of the montane forest belt.

The alpine belt, which extends from c. 3550–4000 m and upwards, is distinguished by the occurrence of thick-stemmed Giant Senecios and Lobelias, woody Alchemillas and a multitude of *Helichrysum* species. On some mountains its vegetation contains *Senecio*-forests and thick "*Alchemilletum*"-carpets, as on Ruwenzori and Muhavura, whereas on Kilimanjaro Giant Senecios are sparse in the alpine belt, which is mostly covered by open and desert-like communities of *Helichrysum* and *Festuca*.

The vegetational differences between the mountains enumerated seem to be due largely to climatic and edaphic divergences, but human influence is certainly also important.¹

Discussion

H. WALTER: Es wird die Frage aufgeworfen, wodurch die Waldgrenze in den Tropen bedingt wird. Die mittlere Jahrestemperatur kann durch die Bodentemperatur in 60 cm Tiefe gemessen werden. Sie ist am Kiliman-

¹ For further information see O. HEDBERG, *Vegetation Belts of the East African Mountains*. Sv. Bot. Tidskr., 45, 1951.

dscharo: untere Waldgrenze 24° C, im Wald 16° C, obere Waldgrenze 10–12° C, obere Phanerophytengrenze 5–6° C. Die Grenze der Frostwechseltage ist höher als die Waldgrenze. Der Wald geht in den Tälern höher als auf den Felsrücken, im SW unter hohen Niederschlägen auch höher als im trockenen NO. Das spricht dafür, das die Waldgrenze nicht durch den Wärmefaktor, sondern durch die geringe Feuchtigkeit der alpinen Region bedingt wird.

O. HEDBERG: In most cases the upper limit of the Ericaceous belt on the mountains seems to be higher on the ridges than in the valleys. Thus in broader valleys the limit is often depressed, whereas it may sometimes be elevated in narrow valleys with good wind protection.

W. LÜDI: In Bezug auf die mittleren Jahrestemperaturen kann man die Waldgrenze in den tropischen Gebirgen nicht mit derjenigen in den Alpen Mitteleuropas vergleichen, wo sie bei einer weit geringeren Mitteltemperatur liegt: In den Tropen alle Monate annähernd gleiche Temperaturen; in den Alpen während der Vegetationszeit gegenüber der mittleren Jahrestemperatur sehr gesteigert. Also in den Alpen bei gleichen mittleren Jahrestemperatur viel günstigere Temperaturen während der Vegetationszeit. Auch macht die ganz verschiedene Flora möglicherweise andere ökologische Ansprüche.

H. DES ABBAYES: Il est à remarquer que dans les montagnes d'A. O. F., l'étage des Usnées se place à une altitude plus basse que dans les montagnes de l'Est africain, soit à partie de 800–1000 mètres. Il semble que le phénomène soit dû au fait que la zone de condensation de l'humidité atmosphérique se place également plus bas en A. O. F. que dans l'Est africain, chose probablement due à une plus grande saturation de l'atmosphère ambiante, nécessitant, pour obtenir la condensation en brouillard, une moins grande différence de température entre le jour et la nuit.

H. HUMBERT: 1) Au sujet de la question de M. DES ABBAYES sur l'abaissement de l'étage à Lichens dans les montagnes de l'Ouest afri-

cain, je pense qu'il est dû aux facteurs climatiques locaux, en premier lieu humidité atmosphérique, condensations occultes, nébulosité, l'altitude n'intervenant que dans la mesure où elle correspond aux exigences des Lichens vis-à-vis de ces facteurs. — Dans les montagnes humides de Madagascar c'est entre 1500 et 2400 m. alt. environ que se présente cette combinaison de facteurs favorable au grand développement des *Usnea*. Au Ruwenzori, sur le versant SW, c'est entre 3000 et 3800.—A Agadir (SW du Maroc, territoire aride), les Lichens foliacés et fruticuleux abondent sur les petits arbres et les arbustes des côtes de l'Océan à 100 ou 200 m. alt. sous l'influence des condensations dues aux vents frais et humides de NW. — Dans le SW de Madagascar (territoire semi-aride, lumineux, ± 300 –350 mm de pluie annuellement) les petits arbres et les arbustes du «bush» xérophile sont couverts de Lichens corticoles dans une bande de territoire, entre 100 et 200 m. alt., non loin de la côte, exposée aux courants aériens humides de S-SW... Ces exemples sont donnés à l'appui de l'opinion exprimée ci-dessus.

2) Au sujet de la biologie des Bambous type *Arundinaria alpina* etc. — Je fais observer que *A. alpina* en Afrique, et divers autres Bambous, sont habituellement des espèces alternantes héliophiles dans la végétation primaire. De leurs stations naturelles (crêtes ou arêtes de montagnes à sol squelettique, bien drainé, elles se répandent dans les brèches ouvertes naturellement ou artificiellement dans la forêt en y formant des peuplements qui représentent un stade d'une série progressive (s'il n'y a pas de nouvelle perturbation) ou régressive (cas habituel quand l'homme intervient par le défrichement et l'incendie).

Les vastes peuplements d'*Arundinaria alpina* sur les pentes des grands volcans éteints d'Afrique équatoriale ne doivent pas être considérés comme un climat climatique. Ils sont liés à des conditions stationnelles

spéciales (physiographiques et édaphiques): pentes de lapilli, cendres et autres sols squelettiques bien drainés). Ils représentent seulement un stade fixé pour une période correspondant au maintien de ce type de station. — Preuve: dès que ces conditions stationnelles changent (pentes moins rapides, sols plus évolués, etc.) on retrouve les espèces caractéristiques de l'étage forestier de haute montagne, telles que *Podocarpus milanjianus*, diverses Araliacées, Myrsinacées, etc., et on voit alors ces Bambous se comporter comme il a été dit plus haut.

A. S. THOMAS congratulated Mr. HEDBERG on his wonderful photographs of these mountains and thought that he was quite right to class the bamboo zone with the forest, for there is evidence that bamboos may spring up when the forest is burnt and that, in time, the forest may spread and shade out the bamboos. Further, it must be remembered that there are great differences between the climate and vegetation of the wet and the dry sides of the mountains, and that the impressions of the vegetation will depend on the side from which the ascent is made.

C. TROLL: Die obere Waldgrenze in den tropischen Gebirgen hat keinen einheitlichen ökologischen Charakter. Sicher gibt es viele Fälle, wo sie eine Trockengrenze ist, z.B. auf niedrigen Bergketten der Grasland-Gürtel, an deren regenexponierten Hängen Feuchtwälder durch Elevationsniederschläge entstehen. Es gibt auch Beispiele, dass in sehr grossen Höhen eine starke Abnahme der Niederschläge erfolgt (z.B. Kilimandscharo), so dass die Trockenheit für die Waldgrenze entscheidend wer-

den kann. In sehr vielen Fällen aber, in denen auch oberhalb der Waldgrenze sehr grosse Feuchtigkeit herrscht (andine Paramos, Ruwenzori, Kenya, Zentral-Neuguinea), ist sicher die Temperatur bestimmend, allerdings nicht die Jahres-Mitteltemperatur, noch weniger Monats- oder Jahreszeiten-Temperaturen, sondern nach meiner Überzeugung das Auftreten der Fröste (oder niedriger Temperaturen) in allen Jahreszeiten. Die Feuchtigkeit kann insofern mitspielen, als in den gegen Wind und Ausstrahlung geschützteren Tälern die Luftfeuchtigkeit die Frostwechsel mildert, so dass die topographische Waldgrenze ein Ansteigen in den Tälern, ein Absteigen auf den vorspringenden Rücken zeigt. Dieses für die Tropen so typische Verhalten gilt aber natürlich auch für die (oberen) Trockengrenzen des Waldes.

WALTER und TROLL diskutierten dann über die Ursachen der Verschiedenheit zwischen Bergrücken und Tälern. Nach WALTER sind die letzteren in der Nacht kälter wegen der abfallenden kalten Luft; nach TROLL ist dies in den Tropen nicht der Fall, da die Strahlung die konvexen Rücken stärker abkühlt.

F. RAWITSCHER: The timberline in the tropics is probably due to different causes; these ought to be examined by ecological methods. Probably water relations in the soil are important.

WALTER sprach über die Bedeutung der Waldbränder für die Waldgrenzen.

TROLL: Die gleichen Phänomene an der Waldgrenze werden auch in feuchten Gebieten gefunden, wo keine Waldbrände angelegt werden.

SESSION 2

Jointly with Section TPH: July 14th, 9 a. m.—noon

Chairman: W. LÜDI, Recorders: G. E. DU RIETZ, E. HULTÉN and H. SJÖRS

SUBJECT:

The Arctic Flora

N. POLUNIN (Montreal)

The Real Arctic

The term 'arctic' has not yet been properly defined for biological purposes, nor has the southern boundary of the arctic region been satisfactorily delimited. The term continues to be very variously applied by different authors in an undesirably vague manner, and the boundary to be diversely placed or inferred. Nevertheless the concept seems important and some form of definition necessary, though no single criterion has been found satisfactory for the delimitation of this vast and varied region. For such purposes as deciding what to include in a preliminary flora of the Arctic now under preparation for *Encyclopædia Arctica* and other works which have long been planned, the real Arctic has been understood as comprising in general the areas of land, fresh water, and adjacent sea that lie north of whichever of the following is situated farthest north in each narrow sector of the northern hemisphere: (1) a line 80 kilometres (50 miles) north of the northern limit of coniferous forest or at least more or less continuous *taiga*, (2) north of the contemporary limit of at least microphanerophytic growth, or (3) north of the Nordenskiöld line. To present a satisfactory overall picture and more workable unit, the boundary has been smoothed out where tongues or outliers suggest that it should be, or in a few places modified in accordance with special knowledge of local conditions.

The arctic region so delimited is of high latitude and treeless, with the winters largely dark and cold and the mean temperature of the warmest month *plus* one-tenth of the

mean of the coldest month over a cycle of years not more than 9° C. even at sea level, with high windchill and less than 50 days between spring and fall frosts, with the subsoil in most places permanently frozen and frost-heaving and allied phenomena important, with an annual precipitation normally below 500 mm (19.8 inches) and mostly in the form of snow which drifts and is packed tightly by the wind, with the soils generally moist in summer but the air of low absolute humidity, and with sheltered salt as well as fresh water frozen over for much of the winter. A map has been drawn to indicate the boundary, and for purposes of range citation the land, especially, lying north of this boundary has been divided into ten major sectors ranging eastwards as follows: (I) Jan Mayen and Svalbard, (II) Franz Josef Archipelago and Kanin Peninsula to the Gulf of Ob, (III) western-central Asia, (IV) eastern-central Asia, (V) easternmost Asia, (VI) Alaska and Yukon, (VII) Canadian Western Arctic, (VIII) Canadian Eastern Arctic, (IX) West Greenland, (X) East Greenland.

At least for treatment of the land vegetation, it seems useful to consider the Arctic as approximately subdivisible into three zones as follows: (1) a low-arctic zone lying immediately north of the southern boundary and having a large and various flora and wide range of plant communities almost always dominated by phanerogams, with vegetation really 'taking hold' of the surface and covering or at least aggressively colonizing most areas of land; (2) a middle-arctic zone forming a belt around the world to the north of the low-arctic zone, and having in most areas a flora reduced by

about one-quarter of the species occurring in comparable low-arctic areas, with a smaller range of plant communities some of which tend to be dominated by cryptogams, and the vegetation barely noticeable from afar except in favoured patches; (3) a high-arctic zone capping the northern hemisphere north of the middle-arctic belt, and having in most areas a flora reduced to half or less of the number of species to be found in comparable low-arctic areas and a vegetational productivity which is still more drastically depauperated, so that the aspect is desolate in the extreme, with the scanty vegetation often consisting largely of cryptogams (especially lichens), struggling for existence in the face of inimical physical forces, and scarcely anywhere modifying the landscape at all evidently. Each zone is further exemplified, and its main plant-sociological and allied characteristics outlined.

As for the flora, about 900 species belonging to some 224 genera of vascular plants are so far known from the Arctic as above delimited, the number of families represented being 63. Many additions must remain to be made through future explorations, or may be recognized as a result of less conservative treatment of certain of the taxonomic entities. Meanwhile provisional details are available of the families and genera so far recorded, with some indication of the distribution within the Arctic of each of the more polymorphic or otherwise problematical groups as well as individual species, and suggestions can be offered as to what might most profitably be elucidated both taxonomically and phytogeographically in the foreseeable future.¹

TYGE W. BÖCHER (Köbenhavn)

The Steppe Vegetation in Continental West Greenland

In the very continental, dry inland in West Greenland (67° n.l.), in close vicinity of the border of the inland ice, a large number of

vegetation analyses have been made in various plant communities. Those made in subarctic or arctic steppe vegetation have now been worked up and a paper dealing with the ecological factors in the continental parts of West Greenland has recently appeared.²

The Greenland steppe vegetation is dominated by xerophilous grasses or sedges which belong to a continental distribution type. On the basis of the occurrence of some species which are more or less exclusive to a certain type of vegetation, the Greenland steppes have been divided into a number of units.

I. Sub- and low-arctic steppe communities (*Artemisia borealis* - *Calamagrostis purpurascens* - *Arctostaphylos* complex).

a. *Carex supina* - *Potentilla Chamissonis* type.

1. *Kobresia myosuroides* group (less xerophytic).

2. *Roegneria violacea* - *Arabis Holboellii* group (more xerophytic; most important sociations dominated by *Carex supina spaniocarpa* and *Calamagrostis purpurascens*).

b. *Puccinellia deschampsiioides* - *Gentiana detonsa groenlandica* type (saline type).

II. Arctic rock and steppe communities (*Carex nardina* - *Lesquerella arctica* - *Dryopteris fragrans* complex).

a. *Carex nardina* - *Hierochloë alpina* type (fell field-barren type).

b. *Saxifraga tricuspidata* - *Dryopteris fragrans* type (rock communities related to the steppe vegetation and the fell field type).

The delimitation of the steppe towards other types of vegetation was made on a floristic basis. It appears that certain communities dominated by dwarf shrubs most naturally belong to the steppe series. *Arctostaphylos uva ursi* forms sociations which belong to the sub- and low-arctic steppe (I) and

¹ The non-taxonomic part of this paper will be published in the *Journal of Ecology* in 1951.

² T. W. BÖCHER: Climate, Soil, and Lakes in Continental West Greenland in Relation to Plant Life. Meddelelser om Grønland, Vol. 147, No. 2. 1949.

Dryas integrifolia dominates sociations which belong to the communities Ia 1, Ib, and II a.

The floristic composition of the Greenland steppe is interesting by its great contents of species with disrupted ranges and very local occurrences in Greenland. This is shown by a number of maps. The gaps in the areas of these species may be due partly to their exclusiveness as regards climate and soil, partly to historical factors (e.g. perglacial survival).

Discussion

R. NORDHAGEN: I ask for the criteria of "steppe" in Arctic regions, because similar vegetation units (*Kobresietum myosuroides*, *Carricetum nardinae*) occur in the mountains of Scandinavia, where they are not or cannot be called "steppe-communities." Is the soil frozen?

T. BÖCHER: The soil is probably not frozen. The definition of "steppe" is phytogeographical. The "steppe-communities" and the alpine communities mentioned are related, and are connected through a series.

A. E. PORSILD: Is there a present deposition of loess? What is the effect on the vegetation?

T. BÖCHER: Loess is still formed. The deposits are very thick. There is much dust on the vegetation. Loess has been formed during very long periods.

C. TROLL: The physiographic and biological conditions in the driest part of Greenland demonstrated by Dr. BÖCHER are very striking and important also for the reconstruction of the Pleistocene landscape in the neighbourhood of the inland ice caps. The arid conditions with drift-sand, loess and salt lakes are connected with the frost actions. Modern physiography distinguishes between arid-aeolian and periglacial-aeolian (as for instance in the humid climates of Kerguelen, Iceland, etc.) conditions. Loess formation is—and in Pleistocene time it was—restricted to districts with glacial and periglacial frost action. If we want to use the term "steppe" we can do it in this part of West Greenland with more

right than elsewhere in the Arctic. But I would prefer to restrict "steppe" to the temperate zones and to say "arid tundra" or "salt tundra" in this case.

A. E. PORSILD: The arctic grassland or prairie in parts of arctic Canada may be comparable with the vegetation described by Dr. BÖCHER.

A. E. PORSILD (Ottawa)

The Vascular Flora of the North American Arctic

The North American Arctic is here defined as the total land area lying north of the tree line which, generally speaking, coincides with the 10° C. isotherm for the warmest month (July). Floristically the North American Arctic may be divided into four major floristic provinces, namely (1) Arctic Alaska and Yukon (2) the Arctic Archipelago (3) continental parts of arctic Northwest Territories and Ungava, and (4) Greenland. In this total area the writer today recognizes 894 species (and varieties of well-defined geographical range) of vascular plants distributed among 60 families and 195 genera. One third of these are widely distributed circumpolar, arctic species.

Arctic Alaska and Yukon—largely unglaciated during the Pleistocene—presents the greatest variety of plant habitats; its flora is rich in isolated and endemic species and undoubtedly is very old. Through its former land connection across hypothetical Beringia there has been a free interchange of species so that almost one third of the present flora of 604 species of vascular plants is of Asiatic affinity. The much smaller number of Cordilleran species may have reached the area by way of the Mackenzie Mountains.

The Arctic Archipelago, comprising all islands lying north of the Canadian mainland, is characterized by a high-arctic climate, and its flora is comparatively poor in species. In his classic monograph of the vascular flora of the Arctic Archipelago, SIMMONS, in 1913, enumerated 204 species. More recently POLUNIN

recorded 233 species inhabiting the easternmost islands. Resulting from the writer's recent investigation of the hitherto little known floras of Banks and Victoria islands, the total number of species now known to occur in the archipelago has been increased to 308 of which no less than 214 were found to occur in Banks and Victoria islands. The Arctic Archipelago was formerly thought to have escaped glaciation. Recent investigations, however, indicate that at least the southern islands have been severely glaciated and that all but the highest parts of the archipelago was submerged in Pleistocene time. Almost one half of its vascular flora consists of widely distributed, arctic species. The presence of a comparatively large number of isolated and endemic species offers some curious phytogeographical problems.

The Arctic Canadian mainland is characterized by a truly continental and very dry climate which, together with the absence of mountain barriers accounts for the striking uniformity and monotony of its plant cover. Of the 651 species now known to occur north of the tree line almost 70 per cent are widely distributed circumpolar, arctic or North American species. A considerable number of non-arctic forest species reach far north of the tree line and, together with tree stumps *in situ* and peat deposits, may indicate past oscillations in the tree line. Owing to the glacial history of this land area its flora is young as indicated by unstable, pre-climax plant communities and by the general paucity of endemic and isolated species. To the west the Mackenzie valley forms a strongly marked floristic boundary which has been crossed by comparatively few species of Cordilleran or bilateral Beringian range.

Greenland, still largely in the ice age, despite its vast extent and range in latitude, harbours a relatively small flora of some 422 species. More than half of these are widely distributed arctic species; a large number may be classed as North American species and about one third as of amphi-Atlantic range.

J. ROUSSEAU (Montreal)

1. Les plantes indicatrices des nunataks dans le Québec

Le remarquable ouvrage de FERNALD intitulé «Persistence of plants on unglaciated areas of northeastern America», publié en 1926 résume l'opinion de l'auteur sur la question et conclut à la non-glaciation d'une partie du territoire entourant le golfe St-Laurent. Des quatre listes de plantes présentées par l'auteur, la deuxième et surtout la quatrième sont considérées comme celles d'indicateurs de non-glaciation. La première groupant des plantes arctiques de la Nouvelle-Angleterre, n'a pas cette prétention. Quant à la troisième, elle grouperait à la fois de plantes indicatrices ou non.

Une connaissance plus étendue de la flore du Québec nous oblige à modifier ces vues. Les listes doivent être émondées pour les raisons suivantes: a) Des espèces ont une aire trop étendue dans l'est du Canada pour servir d'indicateurs. b) D'autres sont introduites ou soupçonnées de l'être. c) Plusieurs sont de simples mutations d'espèces connues dans des régions du Québec ayant subi sûrement la glaciation, de l'avis de tous des partis en cause. d) De nombreuses espèces ne poussent que dans des régions entièrement submergées par la mer Champlain. e) L'aire limitée de certaines est due à conditions lithologiques. f) Enfin, et ce sont de beaucoup les plus nombreuses, plusieurs ont été rapportées par l'auteur de cette communication, du lac Mistassini, des rivières George, Kogaluk et Payne, et des monts Otish, donc de régions situées au coeur même du territoire occupé par le glacier à époque Wisconsin.

Une fois émondées, les listes de FERNALD se présentent ainsi:

	Nombre original d'entités citées	Entités à supprimer	Résidu
Liste I	93	86	7
Liste II	78	76	2
Liste III	65	55	10
Liste IV	293	204	89

Et encore le résidu comprend un certain nombre d'espèces qui n'ont pu être étudiées encore.

Ces faits d'ordre négatif ne démontrent pas que la Gaspésie a subi la glaciation, mais ils indiquent du moins que les plantes ne peuvent servir d'indicateurs de non-glaciation, dans ce territoire du moins. La présence de ces espèces autour du golfe St-Laurent comme au centre de l'Ungava s'explique beaucoup mieux par leur migration le long du couloir désertique bordant le glacier quaternaire: les habitats gaspésiens et les autres du même genre seraient donc, dans cette hypothèse, simplement des avant-postes arctiques ou alpins, suivant les cas.

2. La zone hémiarctique dans le Québec

Dans le Québec, les zones arctique et subarctique occupent deux larges zones occupées respectivement par la toundra typique et la taiga typique. Entre les deux une bande d'environ 200 à 300 kilomètres de large est occupée par un type semi-forestier nommé souvent toundra forestière: alors que le fond des vallées renferme des bandes de taiga, les parties situées à une cinquantaine de mètres ou moins au-dessus de la vallée ne comprennent plus un arbre mais uniquement des formations de toundra, donc arctiques. Les parcelles arctiques couvrent souvent plus de 80 pour cent du territoire. Envisagé à un point de vue quantitatif, cette région est beaucoup plus arctique que subarctique, mais, à cause de lambeaux de taiga au fond des vallées et le fait qu'elle se trouve au sud de la limite absolue des arbres, on la place habituellement dans le subarctique. Dans cette toundra forestière, les habitats de transition entre ceux de l'arctique et ceux du subarctique sont fréquents, mais dans l'ensemble, il y a plutôt de véritables parcelles de toundra, alternant avec de véritables lambeaux de taiga. Vu l'importance géographique de cette bande,

l'auteur est d'avis qu'il y a lieu de lui donner un nom et propose celui de zone hémiarctique.

Discussion

E. DAHL: To the most interesting lecture of Dr. ROUSSEAU I would make some remarks pertaining to the geological side of the question of non-glaciation during the Ice Ages in northern countries. We have certainly had more than one Ice Age. The ice sheet of the last one was probably not the largest. Thus we may find areas left ice-free by the last Ice Age but overridden by ice during the previous ones, and these previous glaciations may have left their marks which we may find. It is therefore of fundamental importance to find criteria by which the marks of the older Ice Ages can be distinguished from those left by the last Ice Age. This problem has been remarkably little considered in geological literature and a closer analysis reveals that the criteria generally used by geologists for this purpose cannot be considered conclusive. As a consequence of this we know very little about the extent of the ice sheets in North America during the Wisconsin Ice Age and in Europe during the Würm Ice Age except for regions where extensive pollen analysis or extensive investigations on the stratigraphy of glacial moraine and interglacial beds have been carried out. It is therefore a dangerous assumption to use as a starting point the thesis that an area like that around the bay of Ungava was totally glaciated during the last Ice Age.

Trying to determine the areas which have been non-glaciated during the previous Ice Ages we meet with the problem about the origin of the boulder fields in the northern countries. This problem is hardly tackled yet and until it has been solved very little can be said about the extension of the non-glaciated areas. The expression "geological evidence," when used with regard to glaciation during the last or previous Ice Ages, should not be taken too seriously.

SESSION 3

July 14th, 1—4 p. m.

Chairman: E. SCHMID, *Recorders: G. E. DU RIETZ and H. SJÖRS*

SUBJECT:

Various Papers

F. RAWITSCHER (São Paulo)
*Climax and Pseudoclimax Vegetation in
the Tropics (South America)*

Recent researches have shown that the majority of tropical savannas, especially in Africa and also in South America, do not represent a natural climax. They must be considered as secondary formations resulting from human interference since prehistorical times (destruction of forests, burning, overstocking). Thus, today's current data on the degree of humidity or aridity of a climate, which would determine the boundary between the natural forest and the savanna, have to be reconsidered, since they are based on the present distribution of savannas and forests. According to SCHIMPER, and to KOEPPEN, the tropical rain forest would require more than 1800 mm of rain a year whereas recent values (AUBREVILLE) approach a limit of 1200 mm. Besides, the length and the distribution of the dry months seem important. In a general way it is supposed that the growth of forests is inhibited by a period of 3 to 4 months of continuous drought.

All these values are more or less of a statistical nature. It is not the dryness in itself but the water available to the plants which really matters. Decisive data will be obtained only through investigations on the water balance of the vegetation involved. Such researches have been made methodically in Southern Brazilian savanna regions which can also be considered as deteriorated forest lands. As is typical for humid tropical regions, the soil is very deep, the undecomposed bedrock lies at a depth of approximately 20 m

and the freatic water level at 18 m. The excess of the summer rains is stored in the ground water and in the soil layers above it; these contain about three times as much water as corresponds to the yearly average rainfall (1300–1400 mm). The drought of four months affects only the surface layers (2–3 m), so that the deep-rooted plants of the campos do not reduce their transpiration even during the most severe drought or hottest hours of the day. Besides, even during the dry period, there is still an excess of water which percolates to the ground water and from there to springs and streams.

The fluctuations of the freatic water level are under observation in a well constructed for that purpose on the highest point of a hill (in order to exclude lateral percolation). The highest level is attained 5 to 6 months after the rainy period, that is in the middle of the dry season; even then gravitative water percolates continuously through the rhizosphere of the deep-rooted plants. The excess of available water shows that *here* the vegetation of savannas is not determined by the aridity of the climate. The annual burnings inhibit the growth of a more luxuriant vegetation. Experiments to exclude burnings have not yet given definitive results.

To sum up, in the humid tropics:

- 1) European agricultural methods lead to rapid deterioration of soils.
- 2) Vegetation on deteriorated soils—burnt yearly—develops into savannas.
- 3) Today's distribution of savannas does not correspond to the ecological conditions.
- 4) Phytogeographical maps based on 3) are not reliable.

5) The ecological conditions must be studied by examining the water balance, considering (a) transpiration, and (b) water available in the soil.

All this is in accordance with data known today for Africa. In the case of Brazil we may add that the campos vegetation does not represent an impoverished forest association resulting from fire. It must be considered as an independent plant formation, which originated in and proceeded from naturally dry regions of Northern Brazil. Thus the tree-forming genus *Andira* is represented by a dwarf form *A. humilis* Mart. which appears above the ground as a dwarf-like bush, while the roots reach a depth of 18 m. The same is true for *Anacardium pumilum* St. Hilaire, *Jacaranda decurrens* Cham., and some Palm trees, as *Acanthococos* sp. These species disappear soon after reforestation with *Eucalyptus*.

Discussion

J. TROCHAIN: La plupart des savanes en régions tropicales humides sont effectivement secondaires. Il faut songer cependant aux savanes primitives qui existent dans les pays tropicaux humides comme dans les pays tropicaux secs où elles constituent alors le climax.

Mais il me paraît difficile de souscrire au quatrième point soulevé par M. RAWITSCHER à savoir qu'une carte phytogéographique ne doit pas tenir compte des savanes secondaires sous prétexte qu'elles ne sont pas l'expression des conditions écologiques.

Ceci est vrai si l'on dresse la carte des climax. Ce n'est plus exact si l'on représente l'état actuel de la végétation car il faut alors tenir compte de tous les facteurs écologiques dont les feux font partie intégrante. On ne peut pas les négliger sous prétexte qu'ils sont d'origine humaine.

En Afrique noire française il existe des types variés de savanes secondaires et toutes sont loin d'avoir la même composition floristique. Certaines contiennent encore des reliques de la

végétation primitive; les autres possèdent des espèces végétales qui sont sous la dépendance des conditions écologiques actuelles au même titre que les espèces primitives. S'il n'en était pas ainsi, toutes les savanes auraient partout la même composition et ne présenteraient pas de différences floristiques.

En résumé on doit tenir compte des savanes secondaires dans une carte phytogéographique de la végétation actuelle, carte qui n'est que l'expression des conditions du milieu. Il suffit de déterminer expérimentalement au préalable le tempérament des espèces caractéristiques ou des plantes indicatrices.

C. TROLL: Die Bedeutung des Problems ist durch die Forschungen von WARMING, BUSSE, PERRIER DE LE BATHIE, LEBRUN, AUBREVILLE u. a. aufgezeigt. Studien über den Wasserhaushalt tropischer Vegetationstypen sind unentbehrlich für die Lösung. Die pflanzengeographische Kartierung jedoch sollte nicht unterschätzt werden. Allerdings darf diese nicht auf den veralteten Begriff der Savanne als eines physiognomischen Types basiert sein. Es gibt Wälder und Grasland im Regenwald-, Feuchtsavannen-, Trockensavannen- und Dornsavannengürtel, abhängig von edaphischen, biologischen und anthropogenen Faktoren. Meine Erfahrung in Ostafrika, wo die klimatischen Typen durch die orographische Gestaltung sehr stark wechseln, ist die, dass man auch aus den Sekundärformationen die Primärvegetation sehr gut erkennen kann. Die in die Grasflur eingestreuten Holzgewächse sind andere im Trockensavannengürtel, andere in der Feuchtsavanne. Auch der Regenwald hat seine besonderen Sekundärformationen, z. B. *Pteridium*-Heide. Wir müssen eben nach ökologischen Vegetationstypen, nicht nach dem Anteil von Gras und Holzpflanzen kartieren.

E. SCHMID: Die Flora deutet auf die Existenz natürlicher Savannen.

F. RAWITSCHER: Es gibt sicher natürliche Savannengebiete, und diese scheinen in Brasilien im „Nordeste seco“, den Trockengebieten der nordöstlichen Staaten, beheimatet zu sein.

H. BOYKO: Ich stimme vollständig mit der Anschauung überein, dass der grösste Teil der Savannen anthropogenen Ursprungs ist. Ich glaube aber, dass wir der tatsächlichen Feststellung der natürlichen Savannengrenzen durch exakte pflanzensoziologische Methoden um vieles näher kommen können. Selbstverständlich dürfen wir bei darauf hinielenden Quadrataufnahmen nicht mit kombinierten Schätzungen von Abundanz und Dominanz arbeiten, sondern mit genaueren Angaben, also mit getrennter Angabe von Abundanz und Dominanz; darüber hinausgehend aber auch mit der Angabe der Individuenzahl der Quadrat, des Entwicklungszustandes (z. B. durch Höhenangaben bei Gräsern), etc. Nur ein derartiges Material kann als Grundlage für statistische Auswertung dienen. Diese Methode, möglichst ergänzt durch physiologische Untersuchungen, dürfte uns am sichersten zum Ziele führen.

H. HUMBERT: Je suis d'accord avec Prof. RAWITSCHER pour estimer très importante la distinction entre savanes primaires et secondaires. Les premières peuvent être climatiques ou édaphiques. Les savanes climatiques correspondent à des climats à longue période de sécheresse et faible pluviosité annuelle (pluies de saison chaude), et forment en gros une zone autour des territoires désertiques; elles occupent de vastes territoires (entre ± 200 et 300 mm de pluies annuellement) en Afrique. Elles n'existent pas à Madagascar (les territoires les plus secs, ± 350 mm, dans le SW, ont pour climax un «bush» xérophile dense). Les savanes primaires sont liées à des sols particuliers (donc édaphiques), ordinairement récents, et fort localisées. — Les savanes secondaires sont dues à l'action de l'homme (défrichements, incendies) et conditionnées par le régime des feux périodiques. On les trouve même sous les climats humides, après de destruction du climax forestier.

La distinction entre savanes primaires et secondaires est beaucoup facilitée par l'établissement du «spectre biologique» et l'examen des parties souterraines. Dans les savanes

climatiques se présentent des plantes de types biologiques (sensu RAUNKIAER) variés. Dans les savanes secondaires peuvent seules se maintenir les espèces susceptibles de survivre à la répétition des incendies (hémicryptophytes dominants; géophytes; parmi les phanérophytes (chaméphytes, ceux-ci rares), seules persistent les espèces capables de se maintenir par rejets, drageons ou de germer et se développer sans souffrir du passage des feux courants (certains Palmiers, etc.). Beaucoup ont perdu la reproduction sexuée. Toutes sont des «pyrophytes».

Pour la cartographie, on peut soit représenter les aires occupées par les types de végétation climatique, soit les aires actuelles de végétation secondaire — soit superposer les deux représentations. C'est seulement une affaire de technique cartographique.

R. DAUBENMIRE (Pullman, Wash.)

A Classification of Forest Associations in the Northern Rocky Mountains

In studying a section of the conifer forest of the northern Rocky Mountains some 100×230 miles in extent, a total of 13 associations have been recognized. The area is unique for the richness of the *Pinaceae*-dominated tree flora (16 species of trees), the complexity of successional relations, and the fact that remnants of primeval forest are still available for study. Some general results are as follow:

(1) Adequate classification of this vegetation demands the recognition of plant associations defined as distinctive combinations of unions (synusia).

(2) Geographic gradients in the structure of the associations are minor, only a very small percentage of the vegetation requiring designation as hybrid in character.

(3) The long-standing practice of most N.A. foresters of classifying forests entirely on the basis of the present composition of the tree union is wholly inadequate for either theoretical ecology or practical land management.

(4) The practice of some northern European foresters and a few in N.A. of classifying forest lands entirely on the basis of subordinate unions is likewise inadequate in the northern Rockies.

(5) Forest potentialities of lands in the northern Rockies cannot be predicted from simple inspection of soil type, topography, and altitude.

Discussion

H. GODWIN: Could Prof. DAUBENMIRE tell us what he takes to be the limits between his associations, since many of them appear to ignore so many of the edaphic factors usually important in differentiating communities; similarly, could he suggest the nature of the factors integrating these communities?

R. DAUBENMIRE: Etiologic work on the causes of the vegetation ecotones is far less advanced than the purely descriptive phase, but I have some evidence that in the lower zones the earliness of onset of drought in summer is critical. In the higher zones where water is always abundant, temperature, leaching, or other factors are probably critical.

M. RAYMOND (Montreal)

Quelques limites naturelles de la flore du Québec, telles qu'indiquées par la distribution de quelques espèces du genre Carex

L'auteur a dressé la carte de chacune des 200 espèces de *Carex* présentes sur le territoire du Québec et, s'inspirant du travail d'ERIC HULTÉN¹ sur les aires équiformes, il a groupé ensemble celles dont les aires étaient semblables. Voici, très succinctement, les phénomènes phytogéographiques qui se dégagent de cette compilation.

1. Les espèces strictement arctiques comme *C. atrofusca*, *C. bicolor*, *C. holostoma*, *C. neurochlaena*, *C. supina*, etc., ont comme limite sud une ligne partant du Cap Jones et remontant le long de la côte de la baie d'Hudson pour

s'engager à l'intérieur du Golfe de Richmond jusqu'à Fort Chimo et sortir sur le Labrador côtier à Okkak.

2. Les espèces arctiques-alpines (*C. Bigelowii*, *C. capillaris*, *C. glacialis*, etc.) fréquentent le même territoire, débordent sur la zone de transition appelée par ROUSSEAU² hémiarctique et se retrouvent plus au sud sur les montagnes de la Gaspésie, de la Nouvelle Angleterre, etc.

3. Il existe aussi des espèces proprement alpines comme *C. atrata*, *C. capitata*, *C. misandroides*, qui viennent jusqu'à la frange arctique, et (3a): des subalpines à caractère méridional comme *C. aenea* et *C. Backii*.

4. Discussion des espèces euryatlantiques: *C. adelostoma*, *C. nigra*, *C. demissa*, *C. Hostiana*, etc.

5. Espèces de l'ouest avec micro-aires dans le Québec et espèce de l'est avec micro-aires cordillériennes.

6. Classification et limites des espèces subarctiques. Comme pour les arctiques, les unes ne sortent pas de leur zone, d'autres se retrouvent plus au sud dans les tourbières du Québec et de la Nouvelle Angleterre.

7. Classification et limites des halophytes: a) à caractère boréal (*C. recta*); b) à caractère méridional (*C. hormathodes*).

8. Une ligne tirée de la baie James le long de la Rupert, passant par le territoire de Mistassini et sortant à l'île Anticosti, constitue une très importante limite nord pour un grand nombre d'espèces tempérées, dont une vingtaine de *Carex*.

9. Des espèces comme *C. argyrantha* dont le foyer de distribution est la région des Grands-Lacs ne viennent que sur quelques points de la rivière Ottawa. Il en est de même de *C. Careyana*, *C. squarrosa*, *C. Davisii* et *C. Sartwellii*.

10. *C. adusta*, *C. ormostachya*, *C. katahdinensis* atteignent le lac St Jean.

11. *C. pallascens* var. *neogaea*, *C. crinita* et

¹ ERIC HULTÉN, Outline of the history of arctic and boreal biota during the quaternary period. Stockholm, 1937.

² JACQUES ROUSSEAU, these Proceedings, p. 614.

quelques autres atteignent par petites colonies isolées les endroits abrités de la Gaspésie, d'Anticosti et le sud-ouest de Terre-Neuve.

12. *C. Crawei*, récolté autrefois sur l'île de Montréal, est absent de l'ouest du Québec, mais fréquent dans la région du Golfe St-Laurent (Anticosti, Percé, etc).

13. Un groupe d'espèces auquel appartient *C. lurida*, *C. conoidea*, *C. granularis*, atteint la ville de Québec.

14. *C. lupulina*, *C. albursina*, *C. blanda*, *C. plantaginea*, *C. amphibola* var. *turgida*, *C. foliculata*, *C. laxiflora*, *C. prasina*, etc., sont inconnus à l'est du lac St Pierre.

15. *C. hirtifolia*, *C. Hitchcockiana*, *C. platyphylla*, *C. Sprengelii*, *C. Grayii*, *C. sychnocephala*, *C. typhina*, communs dans les vallées des rivières Richelieu et Ottawa, ont l'île de Montréal comme limite nord-est. Leur distribution date du retrait de la mer Champlain.

16. Des espèces apalachiennes comme *C. hirsutella*, *C. virescens*, *C. Swanii* ont comme limite nord les bois rocheux qui occupent les confins sud des comtés de Missisquoi et de Brome.

17. Enfin on trouve parmi les laïches du Québec quelques espèces introduites autour des vieux établissements comme Montréal et Québec: *C. hirta*, *C. nutans*, *C. intermedia*, *C. flacca*.

FRANK E. EGLER (Aton Forest, Norfolk, Conn.)

A Commentary on American Plant Ecology, based on the Textbooks of 1947-1949

American Plant Ecology had a dual origin: FREDERIC E. CLEMENTS (botanical survey of Nebraska, 1893) developed the Clementsian system of Dynamic Ecology; and HENRY C. COWLES (University of Chicago, 1895) produced the school of Physiographic Ecology, soon divided into Synecology and Autecology. Later, Mc DOUGALL took some of the features of all three, and developed his own Symbiontology. Coincidentally, four textbooks have recently appeared, which bring into sharp

focus the characteristic traits of each of these four schools. This Commentary reviews the basic principles and concepts adopted in these texts.

CLEMENT's Dynamics of Vegetation (N.Y.: Wilson) reveals his strikingly split personality. Some sections show him as a practical realist, analyzing the problems of soil conservationists, and agronomists; others as an uncompromising idealist, a speculative philosopher who sets up an orderly system of nature, and then forces nature into it. Chapters on "indicators," "climax" and "relicts" reveal the tendency to classify into minute units, using a large number of technical terms based on assumptions of cause-and-effect relationships.

DAUBENMIRE's Plants and Environment (N.Y.: Wiley) is a portrait of the school of Environmental Autecology. By ignoring "conflicting philosophies," he develops his own phase of the controversy: that experimentation upon the various factors of the environment will give us a true knowledge of vegetation. This viewpoint is essentially a reaction from the earlier days of anthropomorphism and teleology, and is based on the almost equally vulnerable supposition that all causes are inherent in the separate factors of the environment.

OOSTING's The Study of Plant Communities (San Francisco: Freeman), is an expression of synecology, deliberately avoids the issues that are controversial, i.e., contrary to his own system. The book leans heavily on an environmental causationism, and on many of the relatively simple philosophic concepts of a generation past.

Mc DOUGALL's Plant Ecology (Philadelphia: Lea & Febiger) expresses his own symbiontology, in which many phenomena of vegetation are classified as various kinds of symbiosis. Otherwise, the book follows the preceding ones.

All four of these books show: (1) an indefiniteness in circumscription of their field of knowledge; (2) a strange naiveness toward the limitations of scientific methodology and ap-

plied logic, and a belief in their own attainment of "truth" and "reality"; (3) the acceptance of an all-out environmental causationism; and (4) an extraordinary isolationism, not only from the literature in foreign languages, but from the British publications and from American work even in very closely related fields.

The paper was read by F. R. FOSBERG.

KARL HÖFLER (Wien)

Durch plasmatische Trockengrenzen bedingte Lebermoosvereine

Der Grundsatz, dass die Vegetationsbeschreibung nicht von einem System der Standorte, sondern von der natürlichen Gruppierung der Pflanzen selbst auszugehen hat, gilt auch für kleine und kleinste Gesellschaftseinheiten. Die Vegetationseinheiten sind nach ihrer floristischen Individualität zu erkennen und abzugrenzen. Wenn sie so erfasst sind, soll die ökologische Untersuchung einsetzen.

Gemeinsam mit TH. HERZOG wurden in einem Regengebiet im Nordrand der Alpen (im Golling städt. Salzburg) die Kalkmoosgesellschaften bearbeitet, die das Kleinklima des Standortes aufs beste widerspiegeln. Vorher waren in Reihenversuchen die Austrocknungsgrenzen der einzelnen Lebermoosarten in kleinen Dampfkammern über H_2SO_4 -Lösungen steigender Konzentration ermittelt worden. Es gibt nicht einfach trockenfähige und trockenempfindliche Moose, sondern die Grenzen stuften sich in langen Reihen ab. Die (primären) Trockengrenzen lagen z. B. für *Aplozia riparia* um 90%, *Lophozia Mülleri* um 86%, *Calypogeia Neesiana* um 82%, *Trichocolea Tomentella* um 70%, *Lophozia quinqueidentata* um 25% rel. Luftfeuchtigkeit (stets bezogen auf 20° C). Die vitalen Trockengrenzen geben die Höchstgrenze des Luftsättigungsdefizits an, die von den Blattzellen der Art ertragen wird. Viele Lebermoose, deren Blättchen mit der Luft in Gleichgewicht stehen, werden so zu Kleinklimaanzeigern. — Ausgenommen sind manche Arten, die auf feuchtem

Substrat mit guter Wasserführung ihr Transpirationswasser nachzuschaffen vermögen, wie *Lophozia incisa* und *Pellia Fabbrioniana*. Man vergl. BUCHS Unterscheidung der ektohydren und endohydren Moose.

Für manche Arten hat sich eine Trockenhärtung des Plasmas nachweisen lassen. Die Lebensgrenzen werden hinaufgerückt — sowohl durch leichtes Vortrocknen im Experiment wie in Trockenzeiten am natürlichen Standort — doch nur bis zu einer oberen, man möchte sagen „absoluten“ Trockengrenze, die für das Plasma der Spezies kennzeichnend ist.

Für einige der bei HERZOG und HÖFLER beschriebenen Moosvereine wird das Vorkommen durch die kritische Trockengrenze einer der Leitarten bestimmt:

Lophozia Mülleri-*Aplozia riparia*-Verein, rel. Feucht. 90–86%

Fissidens adianthioides-*Lejeunea caviifolia*-Verein, rel. Feucht. 70–50%

Pedinophyllum interruptum-Verein, rel. Feucht. 60(–15%)

Otenidium molluscum-*Lophozia barbata*-Verein, rel. Feucht. 25 (–6%)

Härtere Moose können in trockenempfindlichere Verbände eingehen (z. B. das Kalklaubmoos *Otenidium molluscum*), weichere Arten sind von auch nur zeitweilig trockeneren Standorten ausgeschlossen. Eine soziologische Gesetzmässigkeit kommt darin zum Ausdruck, dass viele Moose eben „nahe ihrer Grenze“ zur Dominanz gelangen.

Bei Laubmoosen ist die Bestimmung der kritischen Trockengrenzen methodisch schwieriger. So lag bei *Hookeria lucens* die im einfachen Reihenversuch ermittelte Lebensgrenze bei 80–70% rel. Luftfeuchtigkeit. Doch sterben die stärker getrockneten Zellen hier erst beim Wiederaufweichen. Wie zuerst ILJIN fand, strecken sich die vorher geschrumpften Zellwände und zerreißen den Plasmanschlauch. Das ist „mechanischer Plasmatod“. Bringt man nach ILJINS Vorgang die trockenen Zellen aus den Exsikkatoren zuerst in hypertonische Zuckerlösungen, so lässt sich auch hier die wahre Grenze des plasmatischen Trockentodes

bestimmen; sie lag bei *Hookeria* um 48 % rel. F. — Die Lebermoose sind so günstig für die Bestimmung plasmatischer Austrocknungsgrenzen, weil bei ihnen, vielleicht infolge eines spezifischen Membranfeinbaues, das rasche Wiederanfeuchten der Zellen und Aufquellen des Plasmas schadlos ertragen wird.

Discussion

H. BUCH: Die Untersuchungen behandeln die Trockenresistenz der erwachsenen Zellen. Die embryonalen Zellen zeigen bekanntlich eine grössere Trockenresistenz. Ich stelle mir vor, dass hierfür nicht nur der Zustand des Protoplasmas sondern auch der allen Lebermoosen eigene wässrige Schleim, welcher die Endknospe einhüllt, verantwortlich zu machen ist: es wird sowohl die Eintrocknung als die Wiederaufweichung verzögert.

K. HÖFLER: Auch ich habe Resistenz-Gradienten bei Lebermoosen vielfach beobachtet [vgl. Ber. d. D. Bot. Ges. 60, S. (103)]. Im Reihenversuch hat sich nachweisen lassen, dass es sich bei der höheren Resistenz der plasmareichen Zellen junger Blättchen nicht nur um Vermeidung des mechanischen Trocknendes handelt, sondern wirklich um eine höhere plasmatische Trockenresistenz.

Ihr Hinweis auf die Schleimhüllen der Endknospen ist wertvoll; sie sind sicher ein wirksames Schutzmittel gegen die mechanischen Trockenschäden. Doch wird durch den Schleim der von mir studierte schliessliche Gleichgewichtszustand in den Dampfkammern wohl kaum beeinflusst.

G. E. DU RUIZ: Es ist für uns Pflanzensoziologen sehr erfreulich, dass ein hervorragender Pflanzenphysiologe physiologische Untersuchungen im Rahmen der Pflanzenvereine unternimmt, um die Grenzen zwischen diesen Vereinen ökologisch erklären zu suchen. Eine erweiterte derartige Zusammenarbeit zwischen Physiologen und Soziologen ist sehr erwünscht.

H. MEUSEL: Hinweis darauf, dass die Untersuchungen von Prof. HÖFLER nicht nur für die Soziologie bedeutsam sind, sondern auch für

die Systematik. Die Austrocknungsfähigkeit der Lebermoose ist bei den einzelnen Arten verschieden, also spezifisch. Frage, ob solche spezifischen Merkmale ökologischer Art auch bei den höheren systematischen Einheiten der Bryophyten beobachtet wurden.

K. HÖFLER: Innerhalb der vergleichenden Protoplasmatik hat mich die Frage der „protoplasmatischen Systematik“ seit langem interessiert (vgl. Ber. d. D. Bot. Ges. 1932). Doch liegt an Ergebnissen noch nicht viel vor.

Die Austrocknungsgrenzen und Härtingsgrenzen der Lebermoose erscheinen in der Tat als protoplasmatische Artmerkmale, und ich glaube, diese sind so wichtig wie die morphologischen Merkmale. Die Arten einer Gattung sind oft auch in ihrer Trockenresistenz sehr verschieden. Vollständige Austrocknungsfähigkeit (über 100 % H_2SO_4) wird bei den heimischen Lebermoosen, wie es scheint, nur an wenigen Stellen des Systems (z. B. in den Gattungen *Madotheca*, *Cololejeunea*, dann bei *Marsupella*) erreicht.

W. MEIJER: Ihre Vorlesung hat mich stark interessiert. Am Anfang ist aber eine Frage bei mir aufgekommen, nämlich diese: Braucht man überhaupt derartige autökologische Untersuchungen anzuschliessen an Abgrenzungen von Vereinen, Assoziationen usw.? Kann man nicht einerseits die Autökologie untersuchen und dann weiter nachgehen wie die Arten sich kombinieren können und wie man dann viele ökologische Reihen erkennen kann? Dieses alles würde ohne eine objektiv fast unmögliche Abgrenzung von „Einheiten“ von Moosvegetationen geschehen können.

K. HÖFLER: Ihre Frage ist berechtigt. Ökologische und soziologische Untersuchung kann auch getrennt verlaufen. Die letztere hat aber auch für uns Physiologen grosse Vorteile. So können wir den Standort, dem wir unsere Versuchspflanzen entnehmen, am besten kennzeichnen durch die Pflanzen-Kleingesellschaft, die ihn bewohnt. Z. B. haben sich die verschiedenen „mesomorphen“ und „xeromorphen“ Modifikationen von *Metzgeria conjugata*, mit denen ich arbeitete (vgl. Ber. d. D.

Bot. Ges., 1950), am besten durch die Gesellschaftszugehörigkeit (z. B. zum *Otenidium molluscum*-*Lophozia barbata*-Verein) charakterisieren lassen. — Ferner sind im Hinblick auf

die praktische Auswertung, d. h. zur Kennzeichnung des Kleinklimas, die leicht erkennbaren Moosvereine oft bequemer als die schwer kenntlichen Lebermoose allein.

SESSION 4

Jointly with Section PB: July 17th, 9.30 a. m. — 12.30 p. m., See page 574

SESSION 5

July 17th, 2—5 p. m.

Chairman: L. EMBERGER, Records: G. E. DU RIETZ and H. SJÖRS

SUBJECT:

Phytogeographical Cartography

H. GAUSSEN (Toulouse)

La Carte Internationale à 1/1.000.000 du Tapis Végétal

Du point de vue théorique, il y a de multiples façons d'envisager les cartes botaniques. Mais il est normal que les grandes dépenses que nécessite leur établissement soient justifiées par une utilité économique.

Il est intéressant d'avoir la description de la végétation actuelle, mais il faut savoir comment elle peut se transformer.

En cas de mise en valeur, de défrichement, de reboisement, la notion de dynamisme, de séries ou «phylums» est fondamentale.

Dans la cartographie préconisée ici la classification est dynamique. On détermine les différentes séries aboutissant aux divers climats. Chaque série est affectée d'une couleur. La façon de mettre la couleur correspond aux diverses étapes, aux stades de la série: la teinte plate est la forêt, le quadrillé de lignes est la broussaille touffue, le ligné est le paysage de sous-arbrisseaux, le pointillé est le paysage de plantes herbacées.

Suivant les possibilités offertes par l'échelle, car en cartographie la question d'échelle est primordiale, on peut distinguer des groupements de divers ordres comme les associations ou seulement les grandes «formations».

A une échelle donnée, un groupement n'est représentable que s'il a une surface supérieure à une certaine dimension.

Le choix des couleurs a souvent été fait de façon arbitraire. Il permet pourtant de reproduire graphiquement les conditions écologiques du milieu. Les couleurs peuvent se superposer et permettent une synthèse par leur superposition.

Ainsi, en appliquant la loi du minimum pour tout facteur nécessaire à la vie et la loi du maximum pour les autres, la couleur prépondérante dans la synthèse sera celle des facteurs importants. D'autre part, en donnant des couleurs peu différentes aux facteurs qui ont des actions physiologiques voisines on peut ne pas trop compliquer l'emploi des teintes.

Dans le projet de carte du monde à 1/1.000.000 on a superposé la représentation de six facteurs essentiels:

température, humidité, lumière, facteur xérothermique, période de végétation, sol.

Chacun est affecté d'une couleur ou d'un signe coloré et chaque milieu biologique a ainsi une «formule» qui lui sert de définition.

Deux formules identiques en deux points du monde indiquent une grande analogie écologique.

Les plantes sont donc interchangeables.

La végétation sera donc représentée par la façon de mettre la couleur qui indique l'écologie du lieu qui la porte.

Les mêmes principes peuvent être utilisés pour des échelles plus grandes et des cartes à 1/200.000 sont publiées ou en préparation en France et dans l'Union française.

L. EMBERGER (Montpellier)

La cartographie des groupements végétaux

Les cartes établies sont des cartes des Associations végétales, les Associations étant comprises dans le sens de l'Ecole Montpellier-Zürich. L'échelle choisie est le 20.000°, échelle qui, dans la majorité des cas, s'est révélée la plus pratique. Cependant, dans les cas difficiles, des échelles plus grandes ont été localement adoptées, jusqu'au 5.000°.

Les couleurs et signes ont été choisis de telle manière qu'ils expriment en même temps une idée écologique ou botanique (Exemple, les jaunes pour des associations sèches, les bleus pour des associations humides; la forme schématisée des arbres...)

Le but de cette carte est de servir à la mise en valeur méthodique des sols, les associations étant le reflet du milieu et donnant, par conséquent, des indications sur la vocation des sols.

Les travaux sont entrepris à une grande échelle en Afrique du Nord où un programme de 4 ans prévoit — rien qu'en Algérie-Tunisie — la cartographie de 2 millions d'hectares de terres. En France, l'arrière-pays de Marseille est presque entièrement cartographié entre la Crau-Camargue et Toulon; des cartes ont aussi été dressées pour les régions de Montpellier, Clermont-Ferrand (Auvergne), Frasné (Jura).

Le Luxembourg, qui a décidé la cartographie détaillée du Grand Duché, d'après les mêmes principes, est, à cet égard, directement rattaché à Montpellier.

M. GUINOCHE (Alger)

Assisted in the demonstration of the maps mentioned above.

J. BRAUN-BLANQUET (Montpellier)

La carte de la végétation en Camargue

No abstract obtained.

E. SCHMID (Zürich)

Demonstration von Vegetationskarten kleinen Maßstabes

Die Vegetationseinheiten, welche wir kartieren, sind: der Vegetationsgürtel, die Zusammenfassung aller Lebensgemeinschaften, welche eine Artengarnitur besitzen, deren grösster Anteil einem bestimmten Arealtypus zugehören ob es sich nun um eine Art oder um Vikariante oder um nur einen Teil dieses Areales bewohnende Arten handelt. Für die Darstellung dieser realen grössten Einheit verwenden wir einen kleinen Maßstab, von 1:50000 an aufwärts. Mit den kleinsten Maßstäben können wir nur noch die Zusammenfassungen floristisch verwandter Gürtel, die Vegetationsgürtel-Serien, wiedergeben. Die Herausarbeitung der Vegetationsgürtel wird durch die floristische, insbesondere die chorologische Analyse der Arten erreicht. Die Areale werden nicht nur in der horizontalen sondern auch in der vertikalen Richtung begrenzt. Mit den Klimaxgebieten, dem Klimaxkomplex, der Klimaxformation hat der Vegetationsgürtel nichts zu tun. Er ist keine Successionseinheit. *Abies-Fagus*-Gürtel, *Larix - Pinus Cembra* - Gürtel, *Vaccinium uliginosum - Loiseleuria* - Gürtel, *Quercus pubescens*-Gürtel. Die Zahl derselben auf der Erdoberfläche dürfte etwa gegen 100 betragen. Die Gürtel werden durch Farben bezeichnet. Innerhalb der Gürtelserien wird ein und dieselbe Farbe durch Valeurdifferenzen variiert. Innerhalb der Vegetationsgürtel wird die natürliche Vegetation durch die volle Farbe, die Kulturen durch Auflösung derselben (Punkte, Striche usw.) wiedergegeben, bestimmte regionale und auch lokale Phytocoenosen durch Zeichen.

Die Phytocoenosen, die kleinsten Vegetationseinheiten, sind ebenfalls reale Gebilde. Wir unterscheiden die regionalen Phytocoe-

nosen, welche vorwiegend klimatisch bedingt sind und grössere Flächen innerhalb der Gürtel einnehmen und die lokalen, welche standortsbedingt sind. Die Aufstellung der Phytocoenen wird uns durch die ökologische und biocoenologische Analyse ermöglicht. Für ihre Darstellung haben wir die grossen Maßstäbe nötig von 1:25000 an abwärts. So weit als irgend möglich werden für die zu einem Vegetationsgürtel gehörigen Phytocoenen die Farbe desselben in verschiedenen Valeurs verwendet, für die einzelnen Phytocoenen werden die Zeichen benutzt, Spezieszeichen für die determinierende Art, und Strukturzeichen für die Representationstypen, welche in der Struktur wesentlich sind. Übergänge werden durch Schraffen in den Valeurs der betreffenden Phytocoenen wiedergegeben, Kulturen durch Auflösung der Gürtelfarbe nach Punkten.

Aus den Karten im kleinen Maßstabe können wir Floreneinheiten und ökologische Daten entnehmen; sie sind auch wie Klima-Karten lesbar. Die Karten im grossen Maßstabe liefern uns floristische, ökologische, biocönologische, epiontologische, ökonomische Daten. Sie stellen zugleich Dokumente für die dynamische Forschung dar.

Gezeigt wurden: E. SCHMID, Vegetationskarte der oberen Reusstäler, 1:50000. Beiträge zur geobot. Landesaufnahme der Schweiz Heft 16, 1930. — E. SCHMID, Vegetationskarte der Schweiz 1:200000 herausgegeben von der Pflanzengeographischen Kommission der S.B.G.S.N.G. — E. SCHMID, Halbschematische Karte der Vegetation des Mediterrangebietes. In Berichte der S.B.G. 1950. — E. SCHMID, Vegetationsgebiete der Erde, 1:150000000, aus dem Schwz. Mittelschulatl., Jubiläumsausgabe 1948.

H. GAMS (Innsbruck)

Neue Vegetationskarten aus den Ostalpen

Die Vegetationskartierung hat in den letzten Jahren auch in den Ostalpen gute Fortschritte gemacht. Die Übersichtskartierung nach Art

derjenigen E. SCHMIDS in der Schweiz ist bisher nur im benachbarten Vorarlberg abgeschlossen, in den andern österreichischen Ländern erst begonnen. Aus den meisten liegen bereits neue Spezialkarten in grossem Massstab vor, die teils für wissenschaftliche, teils für land- und forstwirtschaftliche Zwecke aufgenommen worden und erst zum kleinsten Teil gedruckt sind. Für die wissenschaftliche Vegetationskartierung bilden die stereophotogrammetrisch aufgenommenen Alpenvereinskarten 1:25.000 und die für sie benützten Photographien und Autogramme besonders wertvolle Unterlagen.

Als erste Alpenvereinskarte wurde die des Grossglocknergebiets sowohl geologisch wie vegetationskundlich kartiert und ausserdem ihr interessantester Teil um den grössten Ostalpengletscher, die Pasterze, auch 1:5000. Während in der Vegetationskarte des Referenten 44 Vegetationseinheiten durch Farben und Signaturen unterschieden sind, zeigt die neue Spezialkarte FRIEDELs die Verbreitung von 62 Vegetationseinheiten bis zu 3350 m Höhe. Sie ist damit die bisher detaillierteste Vegetationskarte einer grösseren Hochgebirgslandschaft überhaupt und besonders wertvoll dadurch, dass sie eine der grossartigsten, wissenschaftlich interessantesten Gletscherlandschaften noch vor ihrer Veränderung durch gewaltsame technische Eingriffe zeigt. Sie ist nicht nur eine unschätzbare Unterlage für die weitere Erforschung und Gestaltung der Pasterzerlandschaft im künftigen österreichischen Nationalpark, sondern auch allgemein für die Kenntnis der Successionen an zurückweichenden Talgletschern von hohem Wert. In einem Textheft werden die in den 16 Jahren seit der Aufnahme durch natürliche und künstliche Veränderungen ausgelösten Successionen behandelt.

Eine geologische und vegetationskundliche Spezialkartierung 1:10.000 ist im Rofangebirge in den Nordtiroler Kalkalpen durchgeführt worden. Die Autorin der noch ungedruckten Vegetationskarte I. THIMM wird die Interessenten zu Beginn der Alpenexkursion

der Société Botanique de France an Ort und Stelle erläutern.

Von den für Bonitierungs- und Meliorierungszwecke grossenteils im Katastermaßstab 1:2880 von den Wiener Geobotanikern Dr. H. WAGNER, Dr. H. LAUBER u. a. und den Kärntnern Dr. E. AICHINGER, Ing. GAYE, HECK u. a. aufgenommenen Vegetationskarten werden Beispiele vom Vorarlberger Bodenseeufer (1:10.000), von der Ardnung im Ennstal (1:2880), von den oberösterreichischen Donauauen unterhalb Mauthausen (1:5000) und 2 unter Leitung AICHINGERS in Südkärnten (im Lesachtal 1:2880 und an der Villacher Alpe 1:10.000) gezeigt. Die genannten Wiener und Kärntner Kartierer sind vom floristischen Vegetationssystem BRAUN-BLANQUETS ausgegangen, haben sich aber bei der praktischen Arbeit von der Notwendigkeit der Umgrenzung ihrer Einheiten nach Dominanten und Standortseigenschaften und ihrer Anordnung in mehrdimensionalen ökologischen Reihen überzeugt und damit weitgehend den auch vom Referenten vertretenen Anschauungen genähert.

K. HUECK (Tucuman)

Der jetzige Stand der Vegetationskartierung in Argentinien¹

Früher als in anderen Ländern ist in Argentinien vegetationskartografisch gearbeitet worden. Es gibt bereits aus dem Jahre 1876 eine sehr gute Vegetationskarte von P. G. LORENTZ, die bis in die neueste Zeit hinein die Grundlage unserer Kenntnis von der pflanzengeographischen Struktur des Landes geblieben ist. Aus dem Jahre 1893 stammt eine andere Karte von BRACKEBUSCH, die in sehr interessanter Weise die Darstellung der urwüchsigen Vegetation mit der Darstellung der jetzigen Verbreitung der Kulturgebiete aller Art zu verbinden sucht. Überhaupt herrscht in Argentinien ein grosses Verständnis nicht nur für den wissenschaftlichen Wert, sondern auch

für die hohe praktische Bedeutung guter Vegetationskarten.

In dieser Situation war es nur noch ein kleiner Schritt bis zur Schaffung einer planvollen Kartierung des ganzen Landes in einem einheitlichen Maßstab. Eine Karte, die auch die letzten Einzelheiten der Vegetationsverteilung erkennen lässt, muss auch in Argentinien als Grundlage für die verschiedensten Planungen, insbesondere auch für den in der Entwicklung begriffenen Waldbau, eine grosse Bedeutung haben. Als ich nach Argentinien kam, übertrug mir daher der Rektor die Schaffung einer solchen Karte. Von ihr ist das erste Blatt bereits fertig erschienen.

Das geplante Kartenwerk besteht eigentlich aus zwei Karten. Die eine zeigt die Verteilung der natürlichen Vegetation, wie sie ohne den Einfluss des Menschen vorhanden war, und wie sie in weiten Teilen des Landes noch heute anzutreffen ist. Die andere lässt die Veränderungen erkennen, die schon heute durch die menschliche Wirtschaft vorgenommen wurden, insbesondere also die Verteilung des Kulturlandes und die Verbreitung der wichtigsten Kulturpflanzen, den bisherigen Grad der Ausbeutung der Wälder und den Einfluss, den das Weidevieh auf die Waldgesellschaften und auf die verschiedenen Steppenpflanzenvereine hat. Als Grundlage dient die vom Militärgeographischen Institut herausgegebene Karte 1:1 Million. Es sind insgesamt 10-12 Teilblätter vorgesehen.

Auf dem bisher bearbeiteten Blatt Salta — umfassend alles argentinische Gebiet nördlich vom 26° und westlich vom 64° — treten als wichtigste Gesellschaften auf: Chacowälder, laubwerfende Übergangswälder, subtropische Regenwälder, Strauch- und Grassteppen, Salzpflanzen, alpine Rasengesellschaften und reine Wüsten. Insgesamt wurden mehr als 30 Vegetationseinheiten unterschieden und in einem beigegebenen Textheft eingehend beschrieben. Insbesondere von der Verbreitung des subtropischen Regenwaldes und der Zusammensetzung der Vegetation in der Puna vermittelt die Karte ganz neue Vorstellungen insofern,

¹ Not read but abstract distributed.

als das Gebiet des Regenwaldes gegenüber der bisherigen Darstellung erheblich eingengt und in der Puna wesentlich grössere Wüstenflächen als bisher angenommen eingezeichnet werden mussten.

Bei diesen Aufnahmen hat es sich gezeigt, dass selbst in verhältnismässig wenig erschlossenen Gebieten die Aufnahme eines Kartenblattes von 160000 qkm Grösse mit hinreichender Genauigkeit im Übersichtsmaßstab möglich ist, wenn die notwendigen Reisemöglichkeiten geschaffen werden.

Discussion

C. TROLL: Die vorgelegten Karten schwanken im Maßstab zwischen 1:2880 und 1:15000000. Es ist bedauerlich, dass die mitteleuropäischen Vegetationskarten von K. HUECK (1:25000 bis 1:1000000) nicht mit vertreten sind, ferner, dass der Bericht von R. TÜXEN über den Stand der forstlichen Vegetationskartierung in Deutschland in einer anderen Sektion gehalten wurde. Das Hauptproblem sehe ich in der Generalisation. Assoziationen können im Gebirge wohl nur im Maßstab 1:5000, in der Ebene wenigstens 1:25000, dargestellt werden.

Der Vorschlag von Prof. GAUSSEN für eine einheitliche Karte 1:1 Mill. sollte zunächst für Europa in die Tat umgesetzt werden. Es liegen drei Beispiele vor, die Karte 1:1000000, Bl. Berlin von Prof. K. HUECK, verschiedene russische Karten und die Vorschläge von Prof. GAUSSEN vor. Wir sollten zunächst diese drei Methoden diskutieren, um eine gemeinsame Basis zu finden.

W. LÜDI: Der Internat. Bot. Kongress in Cambridge 1930 wählte eine Kommission zu Vorbereitung und Herausgabe einer Vegetationskarte von Europa unter dem Präsidium von Prof. H. BROCKMANN. Er machte verschiedene Vorarbeiten und Versuche zur Kartierung, wobei sich zeigte, dass bedeutende Schwierigkeiten zu überwinden sind. Er berichtete darüber am Kongress in Amsterdam. 1939 ist er gestorben, und die Arbeiten blie-

ben ruhen. Es wäre aber zu empfehlen, sie wieder aufzunehmen, eventuell auf breiterer Grundlage.

H. GAMS: Les cartes russes de KOUSNETZOF, KELLER, etc., en 1:1 Mill. — 1:4 Mill. représentent la végétation en couleurs foncées et les terrains défrichés par les mêmes couleurs plus claires.

H. GAUSSEN, L. EMBERGER, and E. SCHMID also took part in the discussion.

H. GAUSSEN, at the beginning of Session 6, proposed the following resolution, which was accepted by the Section and by the Third Plenary Session:

La Section PHG a proposé la constitution d'une *Commission pour les Cartes a petite échelle* notamment la Carte du Monde à 1/1.000.000¹.

Cette commission serait chargée d'étudier les principes de rédaction de ces cartes représentant les types de végétation et les cultures. Les conclusions de ses travaux seraient présentées au prochain congrès international de botanique.

La Section PHG émet le vœu que cette commission soit rattachée comme sous-commission à la *Commission d'Ecologie et Géographie botanique* créée à Cambridge, elle-même déjà intégrée à la *Section botanique de l'Union des Sciences biologiques*.

Les membres proposés provisoirement seraient: MM. ALLAN, BHARUCHA, CAIN, DANSEREAU, DU RIETZ, GAUSSEN, HUECK, HUMBERT, NEGRI, SCHMID, SUKACHEV, VAN STEENIS, TROCHAIN, TROLL.

M. GAUSSEN assurera la liaison entre les membres et avec l'Union géographique internationale jusqu'à la première réunion où le bureau sera élu.

H. HUMBERT (Paris)

*Une merveille de la Nature à Madagascar*¹

Les territoires montagneux du NE de Madagascar situés entre le massif du Tsaratanana

¹ This paper was read at a special meeting, arranged on July 17th at the same time as the session on cartography.

(2885 m) et l'océan indien n'avaient pas fait jusqu'ici l'objet de recherches botaniques, à l'exception d'un itinéraire suivi en 1912 par PERRIER de LA BÂTHIE dans la vallée supérieure de l'Androranga. Or, entre cette rivière au N et la LoKoho au S, s'étend sur environ 40 km de l'W à l'E et 20 du N au S un massif très escarpé (gneiss et quartzite), le Marojejy, culminant à 2137 m. (altitude déterminée par le capitaine ARRAGON, du service géographique, en 1937), comportant une dizaine de pics à peine moins élevés, tandis que l'altitude des vallées qui l'encadrent n'est que de 400 m. à l'W et de 50 m. à l'E.

Situé dans le secteur où règne la plus forte pluviosité annuelle de l'île (près de 4 m. à Maroantsetra, baie d'Antongil, et sans doute 4 à 5 m sur les pentes de ce puissant condensateur), presque constamment enveloppé de nuages, masqué par les avant-monts, inhabité (redouté des indigènes), ce massif s'est révélé le plus remarquable bloc de nature primitive intacte de Madagascar. Les stations sont diversifiées par la complexité du relief. Les sols (siliceux) sont surtout des argiles latéritiques partout où la pente n'est pas trop rapide; alluvions sableuses dans les talwegs inférieurs des torrents; sols squelettiques ou rochers ailleurs.

Un splendide manteau forestier le recouvre de toutes parts jusqu'aux abords des crêtes, où la végétation devient buissonnante, basse, plus ou moins ouverte sur les bombements rocheux.

Il se situe tout entier dans la *Région orientale* et dans les deux *Domaines de l'Est et du Centre*, subdivisions de cette Région (1). Par suite du régime particulier des courants aériens dans ce secteur, il ne présente pas de contraste entre les versants E et W, ce dernier étant également soumis à des précipitations et à des condensations importantes; mais la vallée de l'Androranga, sous le vent du massif, à la base de ses pentes NW, est nettement plus sèche, et elle a été en grande partie déforestée.

Les facteurs climatiques conditionnent la

superposition de 4 étages de végétation échelonnés altitudinalement. En voici un tableau schématique:

Domaine du Centre

De ± 1850 m. à 2137 m. alt. — Végétation buissonnante à feuilles persistantes, en partie éricoïde, sur les sommets soumis à de rapides variations du degré hygrométrique, de l'insolation ou de la nébulosité, de la température, de la ventilation. Deux biotopes principaux: a) Rochers et pentes bien drainées; b) cuvettes \pm tourbeuses (avec cousins de *Sphagnum*).

De ± 1450 m. à ± 1850 m. alt. — Sylve à Lichens extrêmement dense; arbres (de 5-10 m.) rameux presque dès la base et arbustes surchargés d'épiphytes, avec épais manchons de mousses. C'est le niveau où butent habituellement les nuages et où se manifestent des brouillards persistants; atmosphère généralement très humide; température moyenne peu élevée, assez uniforme ($\pm 15-18^\circ$).

De ± 800 m. à ± 1450 m. alt. — Forêt de montagne toujours verte (de même ci-dessus et ci-dessous); arbres de 12-20 m.; sous-bois très varié, méso-hygrophile, espèces à feuilles tendres, larges; très nombreuses Fougères notamment Cyathéacées).

Domaine de l'Est

De ± 50 m. à ± 800 m. — Forêt ombrophile de haute futaie (3 strates d'arbres) et grandes arbustes, la strate supérieure de 20-30 m., et plus dans les vallons; sous-bois relativement clair et peu fourni. Climat chaud et humide ($\pm 30^\circ$ aux basses altitudes).

Le pourcentage d'endémiques *locales* est de plus en plus élevé à mesure que croît l'altitude: à l'étage supérieur les 2/3 des espèces sont nouvelles et *propres à ce massif* (les autres hauts reliefs ayant tous été explorés). Bien que situé à 100 km seulement du massif du Tsaratanana, très peu d'espèces sont communes à ces deux massifs au-dessus de ± 1850 m.

Les avant-monts les plus élevés, autour du Marojejy, ont fourni un contingent d'espèces non vues dans le massif principal.

¹ Cf. H. PERRIER de LA BÂTHIE, *La Végétation malgache* (Ann. Muséum colonial de Marseille, 1922). — H. HUMBERT, *Principaux aspects de la Végétation à Madagascar* (Mém. Acad. malgache, Tananarive, T. IV, 1926).

Au total le nombre des espèces (linnéennes) découvertes par l'auteur de cette note en 5 mois de séjour dans ce secteur (nov. 1948 à avril 1949) est compris entre 200 et 300, dont (parmi les familles déjà étudiées) 40 orchidées, 30 Composées, 30 Balsaminacées, . . .

Ainsi se confirment l'extraordinaire richesse de cette flore insulaire, et l'étroite localisation d'une foule d'espèces, ce qui s'explique:

a) par l'antiquité des territoires de l'île, surtout dans l'Est et le Centre (fragment du continent de Gondwana).

b) par des connexions, échelonnées du Crétacé supérieur au miocène, avec diverses parties du globe (d'où peuplement par des éléments d'origines diverses).

c) par l'absence de grandes perturbations climatiques depuis l'ère tertiaire.

Une proposition de classement en *Réserve naturelle intégrale* (50.000 Ha.) a été soumise au Conseil supérieur pour la Protection de la Nature en France. La procédure de classement suit son cours. Ce sera la 12^e Réserve naturelle de Madagascar.

SESSION 6

July 18th, 9 a. m. — 1 p. m.

Chairman: K. FAEGRI, Recorders: G. E. DU RIETZ and H. SJÖRS

SUBJECT:

Quaternary Vegetation and Flora

W. LÜDI (Zürich)

Interglacial Woods of the Swiss Plateau

During the maximal extension of the glaciation the Swiss plateau was totally glaciated, during the last glaciation only for the larger part. Therefore diluvian deposits can be found everywhere. But it is often difficult to distinguish the deposits of glacial and interglacial time and even more difficult if not impossible to attribute the interglacial deposits to a certain interglacial time.

The best indicators of interglacial time are remains of trees. They have been found in layers of tuff, gravel or loam and especially in the remains of interglacial mires, called lignite or *Schieferkohlen*. The woody remains in the lignite are mostly *Pinus*, *Picea*, *Betula*, rarely *Alnus*, *Corylus*, *Quercus*, therefore indicators of a coniferous forest, whilst in mineral deposits more remains of broadleaved trees as *Quercus robur*, *Acer pseudoplatanus*, *Corylus*, *Tilia platyphyllos*, *Tilia cordata*, *Alnus incana*, *Fraxinus excelsior* and others have been found.

The remains in mires and in tuffy or loamy layers are always of a local significance.

The pollen analysis gives us means to study the composition of interglacial woods and especially that of the regional forests, to some degree independent of the local factors which brought about the conservation of the organic macrofossils. I have examined the pollen content in nearly all the Swiss interglacial layers known, especially in those of lignite. Generally the diagrams represent clearly only a part of one interglacial period. They are very similar: dominant pollen of Conifers (*Picea* and *Pinus*, sometimes abundant or dominant *Abies*). Pollen of broadleaved trees are scarce, often absent. Rather regularly *Betula* and *Alnus*, the latter dominant in some horizons of several localities. Other pollen of broadleaved trees: most frequently *Corylus*, sometimes *Quercus*, *Ulmus*, *Tilia* (*Tilia cordata* seems to be preponderant), *Carpinus*, *Juglans*, rarely *Salix*, *Ostrya*, *Castanea*, *Fagus*, *Fraxinus*, *Acer* and *Hippophaë*. In the tuffs of Flurlingen and in the interglacial sediments

of Geneva, the pollen of broadleaved trees was ordinarily more frequent, but conifer pollen was always dominant. *Fagus* pollen was found in the uppermost layers of the alluvions anciennés of Geneva and of the tuffs of Flurlingen. The contents of tree pollen in the sediments was generally of medium magnitude. Pollen of herbs and grasses were always scarce, often absent.

The pollen spectra of all examined interglacial deposits represent a coniferous forest with hygrophilous woods on moist soil and some mesophilous broadleaved woods in favourable situations. They seem to correspond to a climate a little more continental than that of today, comparable to the climate of the temperate East of Europe. The *Abies* dominance with copious pollen of broadleaved trees may indicate a period of more favourable climate and the mentioned appearance of *Fagus* may be the consequence of some variation of the climate in the oceanic direction.

Geologists assign the examined interglacial deposits to several interglacial periods, the greater part to Riss I–Riss II (Durnténien). Our pollen diagrams do not allow us to distinguish the interglacial periods from each other. If the deposits were really formed during several interglacial periods, the woody vegetation of the younger part of the diluvial period would have been rather uniform.

F. FIRBAS (Göttingen)

Die quartäre Vegetationsentwicklung zwischen den Alpen und der Nord- und Ostsee¹

Die quartäre Vegetationsentwicklung Mitteleuropas war infolge seiner Lage besonders reich gegliedert. Nennenswerte subarktische Waldgebiete haben hier die letzte Eiszeit und sicher auch die Mindel- und Risseiszeit nicht überdauert, die in ihrem Verlauf noch unbekannte polare Waldgrenze lag damals südlich der Alpen. Sie war stärker herabgedrückt als die Schneegrenze, ein Beweis für Niederschlags-

armut. Steppenartige Züge der Glazialvegetation kommen u. a. in hohen *Artemisia*-Anteilen zum Ausdruck. Deren Maxima fanden sich aber bisher überraschenderweise nicht in den Zentren der Lössablagerung oder in den heutigen Trockengebieten, sondern in den Alpen und im Alpenvorland.

Die spät- und postglaziale Waldgeschichte wurde vor allem durch zwei grossräumige Klimaschwankungen beeinflusst. Der stadiale Klimarückschlag der jüngeren Dryaszeit hat die Wälder in den meisten Landschaften nochmals zurückgedrängt. Da er mit einer Zeit hoher sommerlicher Strahlung zusammenfällt, mahnt dies gegenüber der Strahlungskurve zur Zurückhaltung. Die postglaziale Wärmezeit ist auch in Mitteleuropa als solche völlig gesichert. Sie ist allmählicher ausgeklungen, als man früher annahm. Die Waldentwicklung ist im übrigen allein durch die Klimaentwicklung kaum zu erklären. Die im Gegensatz zur raschen Ausweitung der Arealgrenzen merkwürdig langsame Massenausbreitung der Gehölze führt zur Frage nach den gleichzeitigen Veränderungen im Biotypengehalt der Arten.

Der grösste Teil des neolithischen und bronzezeitlichen Siedlungslandes ist bereits dem Wald abgewonnen worden. Die mittelalterliche Erweiterung der Siedlungsgebiete spiegelt sich in den Pollendiagrammen besonders deutlich wieder und gestattet einen pflanzensoziologisch lehrreichen Vergleich zwischen dem vorhergehenden Waldzustand und dem heute als „natürlich“ angesehenen. Diese mittelalterliche Landnahme ist vielfach auf Kosten *Carpinus*-reicher Wälder erfolgt.

Bei der Betrachtung der Interglaziale interessieren (abgesehen von dem allmählichen Ausklingen des pliozänen Elements) vor allem zwei Fragen: die Veränderungen beim Herannahen der nächsten Vergletscherung und die Ursachen der Verschiedenheiten gegenüber dem Postglazial. Zunehmende Vermoorung, eine sehr späte Ausbreitung von *Abies*, ansteigende Ericalen-Werte u. a. zeigen, dass mit dem frühglazialen Temperaturrückgang zunächst die Ausbreitung einer montan-borealen

¹ Ausführlicher in *Erdkunde* (Bonn), Bd. 5, S. 6–15, 1951.

und später subarktischen Vegetation mit höheren Feuchtigkeitsansprüchen vor sich ging. Die Humidität ist dann wahrscheinlich bis weit ins Spätglazial immer mehr zurückgegangen. Die bekannten Besonderheiten der letzten Interglaziale (weitere Ausbreitung von *Abies* und *Picea*, Vorherrschaft von *Carpinus* anstelle von *Fagus*) lassen sich kaum allein durch veränderte regional-klimatische Bedingungen erklären. *Fagus sylvatica* scheint vielmehr erst im jüngeren Diluvium die Biotypen entwickelt zu haben, die zu einer Massenausbreitung nötig waren. Die Stellung einiger „*Fagus*-Interglaziale“ ist noch zu klären.

Discussion

P. W. THOMSON: Die mittel- und oberpliozänen *Fagus*-Formen unterscheiden sich was Blattrand, Früchte und Pollen anbetrifft deutlich von *Fagus sylvatica* im mitteleuropäischen Raum. Es ist nicht ausgeschlossen, dass in N. Deutschland pliozäne Ablagerungen für interglaziale gehalten worden sind.

F. FRIBAS: Leider ist das von C. A. WEBER untersuchte buchenführende Interglazial von Fahrenkrug in Holstein (die Buche ist hier auch makroskopisch nachgewiesen) pollenanalytisch noch nicht genauer untersucht worden. Es ist aber sehr wohl möglich, dass es dem älteren Diluvium angehört.

F. FLORSCHÜTZ (Velp)

On the Vegetation in the Netherlands during the Last Glaciation

In the course of the last glaciation, water and wind built up a sequence of chiefly fine-grained layers in the Netherlands, the so-called Lower Terrace. In several places this complex is underlain by marine and terrestrial Eem-deposits and covered by holocene, beginning with preboreal, sediments. The time during which the "Lower Terrace" was formed has recently been called Tubantian, thus using a word derived from an old Dutch landscape-name.

Large excavations in the "Lower Terrace," both in the eastern and the utmost western parts of the country, made possible the collection of material for studying the macroscopic and microscopic remains of the Tubantian flora.

Notably the results of palynological analyses made it evident that the division of the last glaciation into three stadial and two interstadial phases is likewise applicable to the Netherlands.

However, the circumstances did not always allow to assemble separately the macroscopic plant-remains from stadial and interstadial deposits. Consequently, the Tubantian flora must for the time being be regarded as a whole, the first aim consisting in tracing its phytogeographical elements.

Efforts in that direction have led to a provisional distinction of some groups of plants, among which a small "steppe" group is conspicuous. Its members were particularly well represented in a lenticular bed of plant-remains, probably formed at the end of the last interstadial or the beginning of the last stadial phase. It is remarkable that the loess occurring in some parts of the province of Gelderland is presumably a product of the same time.

Discussion

P. W. THOMSON: In Esthonia *Polygonum viviparum* occurs in multitude on wet humid soils together with *Selaginella selaginoides* and *Saussurea alpina*.

K. JESSEN and F. FLORSCHÜTZ also took part in the discussion.

T. VAN DER HAMMEN (Leiden)

Die spätglaziale Vegetationsentwicklung in den Niederlanden

In der letzten Zeit haben wir eine bessere Einsicht gewonnen in die spätglaziale Vegetationsentwicklung in Holland. Nach der ersten Erkennung der Allerød-Oscillation in Holland in Gyttja-Ablagerungen aus der Provinz Drenthe (1948), wobei die Entwicklung der

Vegetation mit der Pollenanalyse festgestellt werden konnte, war es unschwer auch sonstwo in diesem Land eine ähnliche Vegetationsentwicklung festzustellen an Hand neuerer Analysen von spätglazialen Torfschichten und Seeablagerungen. Die Allerød-Zeit zeigt sich immer als eine Periode mit fast völliger Bewaldung, zu Anfang fast nur mit *Betula*-Wäldern, wonach *Pinus* recht bald ein wichtiger Bestandteil in der Walddzusammensetzung wird. In der älteren und in der jüngeren Dryas-Zeit muss die Vegetation ziemlich offen und spärlich gewesen sein: spätglaziale Torfschichten, eingeschaltet im „Treibande“, scheinen sich in der Allerød-Zeit gebildet zu haben, dagegen fand also in der älteren und jüngeren Dryas-Zeit Sandtransport durch Windwirkung statt.

Die Bölling-Oscillation (zum ersten Mal nachgewiesen von IVERSEN in Mittel-Jütland), konnte auch in Holland an verschiedenen Stellen nachgewiesen werden, und ist dann meist besonders deutlich. Die von FLORSCHÜTZ auf Pflanzenreste untersuchten Ablagerungen von Almelo (worüber er berichtet hat) befanden sich in sandigen Schichten. Durch die Analyse einer sich darüber befindenden Torfschicht konnten diese Schichten datiert werden als älter als die Bölling-Oscillation.

Es zeigt sich ein ausgesprochener Unterschied zwischen der Vegetation in der älteren und in der jüngeren Dryas-Zeit. In der älteren Dryas-Zeit scheint *Pinus* fast ganz abwesend zu sein. *Artemisia*, *Helianthemum*, *Hippophaë*, *Rumex*, *Chenopodiaceae* waren allgemein verbreitete Pflanzen. Ferner liessen sich u. a. *Sanguisorba minor* und *S. officinalis* feststellen. Letztere Art ist auch interessant, da sie heute im skandinavischen arktischen Gebiet fehlt, jedoch häufig ist im alpinen Gebiet. Während in der älteren Dryas-Zeit mehrere Pflanzen allgemein vorkommen, die auf ein „Steppencharakter“ der Vegetation zu weisen scheinen, kommen diese Arten viel weniger oder gar nicht vor in der jüngeren Dryas-Zeit. Dagegen ist dann eine starke Verbreitung von *Empetrum* charakteristisch. Dieses weist möglicherweise auf einen mehr

atlantischen Character des Klimas in dieser Zeit, worauf auch das Fehlen, bzw. das spärlichere Vorkommen, der „Steppenelemente“ hinweisen könnte.

Es ist wahrscheinlich, dass auch der Mensch schon einigen Einfluss auf die Vegetation ausgeübt hat während des Spätglazials, sei es nur an einzelnen Stellen und nur in geringem Masse. Hierauf scheint jedenfalls das Pollendiagramm einer Gyttya-Ablagerung (zu Usselo), worin eine Kulturschicht anwesend war, zu deuten. Der *Pinus*-Wald in der Umgegend scheint abgebrannt zu sein, wodurch für kurze Zeit *Betula* die Oberhand bekam. Zu gleicher Zeit zeigen die *Chenopodiaceae* ein kleines Maximum. Diese müssen hier also sehr wahrscheinlich als „ruderal“ aufgefasst werden.

Discussion

F. FIRBAS: In Ostpreussen hat H. Gross an verschiedenen Stellen eine Auslaugung der Böden unter den Wäldern der Allerødzeit und kalkarme Schwemmlehme während der jüngeren im Gegensatz zu kalkreichen während der älteren Dryaszeit festgestellt. Trotzdem spielt dort *Empetrum* in der jüngeren Dryaszeit keine nennenswerte Rolle. Das bestätigt die Ansicht Herrn VAN DER HAMMENS, dass die Ausbreitung der *Empetrum*-Heiden während der jüngeren Dryaszeit auf klimatische Veränderungen und nicht auf eine Auslaugung der Böden zurückgeht.

I. HIITONEN: Die Art *Sanguisorba officinalis* L. kommt noch im arktischen Teil Fennoscandias vor, nämlich als var. *polygama* (Nyl.) M. & C. auf der Halbinsel Kola, wie es auch aus dem Kartenbuch HULTÉNS hervorgeht (1950, S. 277).

G. F. MITCHELL: Seeds of *Chenopodium rubrum* have been found in younger Dryas deposits in Ireland, when there was no suggestion of human influence.

JOHS. IVERSEN: Chenopods in late-glacial time certainly grew independently of man; on the other hand they must have found ideal

conditions on the sites of the mesolithic settlements, just as we know they did in post-glacial time.

K. JESSEN also took part in the discussion.

H. GODWIN (Cambridge)

The Late-Glacial Vegetation of Great Britain

In considering the Late-Glacial vegetation of Great Britain a distinction is made between deposits which are known to be of approximately Allerød age and which extend to the beginning of Post-Glacial time, and deposits which are pre-Allerød but later than the maximum of the last glaciation.

The older category of deposits includes certain species of plants now extinct in the British Isles: apart from *Betula* and *Pinus*, trees are not represented in the vegetation, which, however, is of the grass-sedge tundra type with most of the herbaceous flora characteristic of the later Allerød time.

The Allerød is represented by various stratigraphic facies, but the pollen assemblages are very similar to those of Denmark to the east and Ireland to the west. The highly recognisable pollen grains of *Polemonium coeruleum* have been recorded from eight Late-Glacial localities in different parts of Great Britain, from widely beyond the present restricted range of that species. The pollen identifications have been supplemented by the recognition of considerable numbers of seeds, fruits and larger remains. In the aggregate lists of species the chief categories represented are: (a) "Arctic-alpine," which are now much restricted in range, for example, *Betula nana*, *Salix herbacea* and *Thalictrum alpinum*; (b) Aquatic and Marsh plants, which in general are not very strongly indicative of climatic conditions; (c) Woody plants, such as *Juniperus*, *Sorbus*, bush willows and tree birches; (d) Abundant Ruderals and Weeds, including some hitherto regarded as introduced to Britain by prehistoric man, for example, *Linaria vulgaris* and *Galeopsis tetrahit*; (e) A small group of species of Atlantic character, such as

Calluna vulgaris, *Andromeda polifolia* and *Erica tetralix*. It is concluded that conditions in Late-Glacial times were exceptionally favourable to rapid migration of species which favoured open habitats but which did not have exacting demands for warmth. Many features of present day distribution must be regarded as due to restriction of range through the extension of forest and peat-mire in the warm Post-Glacial period which followed the open conditions of the Late-Glacial times.

Discussion

G. E. DU RUIZT: The lists of species given by Dr. GODWIN are a very valuable help for those who are trying to understand the general European background of Scandinavian Late-Glacial vegetation. They could perhaps become still more valuable if the list of "Arctic-alpine" species, now founded exclusively upon the present distribution in Great Britain and Ireland, was differentiated with consideration to the present distribution in Scandinavia into (1) one group of plants that are now restricted to the mountain regions and their neighbourhood also in Scandinavia, e.g. *Dryas*, and (2) one group of plants that are now distributed over at least most of the Scandinavian lowlands, thus having an indicator value very different from that of group (1), e.g. *Arctostaphylos uva-ursi*, *Calla palustris* and *Rubus saxatilis*.

F. FLORSCHÜTZ: Dr. GODWIN has spoken of *Linum praecursor* Reid as an extinct, doubtful species. If I am not wrong, Miss REID in a recently published paper has united that species with *Linum perenne*. Is there sufficient difference between the seeds of these species?

G. ERDTMAN: As to pollen morphology in *Polemonium*: the pollen grains in *Polemonium boreale*, *P. coeruleum*, and *P. acutiflorum* can be distinguished from each other. Distinctions can also be made within *Artemisia* and we are looking forward to contributions from the British Isles in solution of the highly interesting and important "Artemisia problem."

R. NORDHAGEN: *Arctostaphylos uva-ursi*, which Dr. GODWIN listed as an "atlantic" species, is not atlantic or oceanic in Scandinavia. In fact it is more common in the continental than in the oceanic parts of the Scandinavian mountain range.

H. SJÖRS: In Dr. GODWIN's list of "Ruderals and Weeds" in Late-Glacial deposits some plants are included that occur in truly natural meadow and meadow forest vegetation in Fennoscandia, viz. *Cirsium heterophyllum*, *C. palustre*, *Ranunculus acris*, and *Rumex acetosa*. In addition, we have indigenous races of *Leontodon autumnalis*, *Taraxacum*, etc., in mountain grassland.

I think there must have been a certain element of meadow species in the British Late-Glacial flora, and occurrences of meadow-like communities in the vegetation.

W. LÜDE: Wir bekamen heute von Dr. GODWIN und anderen Vortragenden Fundlisten aus dem Spätglazial NW-Europas vorgelegt, aus denen auch der im alpinen Gebiet arbeitende Pflanzensoziologe gewisse Arten anders zuordnen würde. Doch würde eine eingehende Diskussion dieser ökologischen Verhältnisse jetzt zu weit führen.

H. GAMS: Which species of weeds could be connected with giant deer and other big mammals?

J. IVERSEN: The occurrence of "weeds" in late-glacial time is certainly remarkable. Some of them may subsequently have been exterminated by the advance of the forest, and later reintroduced by man. This applies to *Centaurea cyanus* in Denmark.

(In reply to a question by R. NORDHAGEN.) Weeds grow luxuriantly around the hunters' settlements in Greenland; ruderal Chenopods, however, are not found so far North.

H. GODWIN: The grouping into geographical range lists was very provisional and must be fully reconsidered when the lists are full and representative.

The identification of *Plantago lanceolata* was based upon pollen; there had been no comparison of the *Polemonium* pollen with

that of *P. acutiflorum* or *P. boreale*; the pollen of *Empetrum* appeared to be that of *E. nigrum*.

K. FÆGRI also took part in the discussion.

J. IVERSEN (Charlottenlund, Denmark) *Origin and Postglacial Development of the Flora of West Greenland in the Light of Pollen Analysis*

Greenland forms a bridge between the old and the new world; and so the problems regarding the origin of the flora of Greenland are of general interest. Extreme opinions in this respect have been put forth ranging from the "tabula rasa theory" to the assertion that up to 100% of the flora might have survived the last glacial epoch on unglaciated mountain peaks ("Nunataks"). But up to the present date no empirical investigation of the actual development of the vegetation in Greenland has appeared.

The present pollen analytical investigation is a preliminary contribution to make up this deficiency. The material has been gathered by borings from pontoons in a number of lakes in a large succession of valleys at the head of Godthaab Fjord.

The development of the vegetation may be divided into 5 well defined epochs. In the 1st lengthy epoch a rich flora of herbaceous plants and dwarf bushes occurs, but shrubs are totally absent. The commencement of the 2nd epoch is fixed at the arrival of the larger *Salices*; shortly after *Alnus viridis* also immigrates. The 3rd epoch is extremely sharply marked by the immigration and the dynamic expansion of *Betula nana*. Almost simultaneously *Juniperus* immigrates. The 4th epoch is the post-glacial warm period in Greenland, characterized by the domination of *Alnus*, and ample pollen of *Myriophyllum alterniflorum*. Finally, the 5th epoch is stamped by the deterioration of the climate; *Alnus* recedes and *Myriophyllum alterniflorum* becomes sterile. In this epoch the Icelandic Vikings settle here, and this event is sharply registered in the pollen diagrams by the progress in grasses and herbs

to the cost of *Salix* and *Alnus*. On the withdrawal of the Norsemen, the shrubs regenerate.

When the bottom layer in the lakes was deposited, the borderline of the ice had withdrawn from the outer coast to its present extent. The demonstration of several thermophilous water- and marsh-plants (dispersed by birds!), and pteridophytes (dispersed by air currents!), in the bottom layer, shows that the climate was almost as warm as in our time. The fact that thousands of years elapsed before *Betula nana* and *Juniperus* immigrated to the region signifies that these plants have not survived the last glaciation in the nunataks of Western Greenland. On the other hand, it is remarkable that *Papaver*, *Dryas*, *Salix herbacea*, and other plants whose long-distance dispersal is scarcely better than that of birch and the large willows, have been demonstrated in the earliest deposits. This is an indication that the distinctly arctic plants have survived the last glaciation in Greenland.

Discussion

T. W. BÖCHER: Greenland is more a continent than an island. It may be difficult or impossible to reach any general conclusions regarding the survival of southern plants in Greenland from evidence from a single area in the Godthaab district.

Southern species may have survived in oceanic half-nunataks (capes) or in continental tundra-refugia north of the Godthaab fjord region. *Betula nana* may be represented in Greenland by relatively arctic biotypes; it is absent from southernmost Greenland and reaches high latitudes.

The very interesting pollen-analytic data from Godthaab fjord must be synthesized with all facts that appear from recent plant distributions, and which make a survival during the last ice epoch probable even for southern plants.

J. IVERSEN: The absence of *Betula nana* in the southernmost part of Greenland may be

explained by the presence there of the closely related *Betula glandulosa*. This and other American species are certainly the sources of long-distance transported *Betula* pollen before the immigration of *Betula nana* to Greenland.

A. E. PORSILD: 1. In relation to the age of the present flora of Greenland I suggest a certain correlation between the distribution of the Amphi-Atlantic element in the flora in Greenland and in Eastern N. America. This element is abundantly represented in Ungava and the eastern islands of the Arctic Archipelago but does not extend west of Hudson Bay where only a few species are found.

2. May I ask Dr. IVERSEN to state if by "Nunatak" he meant "alpine peaks protruding above large continuous sheets of ice," or if he merely meant "every icefree land area surrounded by ice."

N. POLUNIN: The paper is of particular importance in view of the paucity of studies of arctic regions of this nature, and raises far too many points of interest than can be discussed briefly. Among incidentals I would mention (1) the recent publication on winged Abietinean pollen in the air of West Greenland, (2) the significance of the observations concerning the carrying of disseminules by birds which, like plants, have marked habitat preferences, and (3) the suggestion that *Sisyrinchium montanum* may have been introduced from America by the Norsemen. There appear to have been other plants so introduced from the West, quite apart from the several previously postulated as transported from the East.

R. NORDHAGEN: If the birds leave for instance Iceland in early spring, the landscape there might be snow-covered, and it is difficult to understand how an effective seed transport can occur at that time of the year. Most plants have seeds and fruits in the autumn.

A. E. PORSILD: In connection with the part played by birds as agents of plant distribution I doubt the importance of geese because these birds migrate in a very orderly manner and

travel almost with "timetable" regularity. On the other hand ptarmigan migrate step-by-step and are often carried out to sea when lost in snowstorms or fog. It is well known to residents in West Greenland that late in autumn large flocks of ptarmigan during S.W. gales arrive from the West in exhausted condition. I have personal knowledge of cases where large flocks of ptarmigan have landed on the decks of ships in the middle of Davis Strait, in Hudson Strait and in Hudson Bay or even off the coast of Labrador. Ptarmigan travelling in this manner undoubtedly may carry undigested seeds in their crops. The distribution in W. Greenland of *Arctostaphylos alpina*, *A. uva-ursi*, and others, strongly suggests that they may have been brought by ptarmigan. Each year a large number of birds, not native or indigenous to the avifauna of Greenland, land there during southwesterly gales. Like the ptarmigan they were accidentally carried there by the gale and may well carry plant seeds in their crops.

G. F. MITCHELL (Dublin)

Naias flexilis (recent and fossil) and
Naias marina (fossil) in Ireland

N. marina does not grow in Ireland to-day, but *N. flexilis* is recorded from a number of lakes, usually small, along the western margin. More intensive search would probably reveal many more localities. Most of the localities occur on non-calcareous rocks where soils are thin, and the lake waters are relatively oligotrophic. *N. flexilis* does grow in the large Lower Lake at Killarney; part of this lake lies on limestone and one of the rivers which feeds it brings in alkaline water; in this lake conditions are relatively eutrophic.

It will be noted that the fossil finds also occur towards the north and west of the country. Lake-basins in the centre and south-east have been examined but no finds have been made in these areas. Most of the finds occurred in oligotrophic algal-mud; at two localities *N. marina* occurred in a calcareous

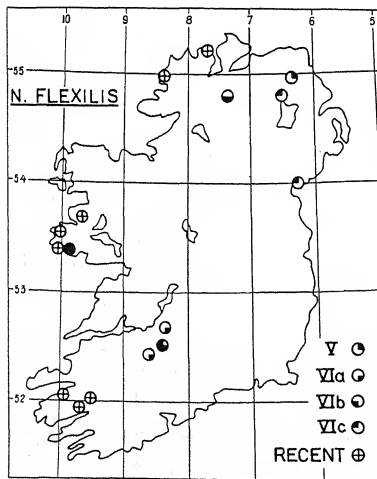


Fig. 1. Localities for *Naias flexilis* in Ireland.

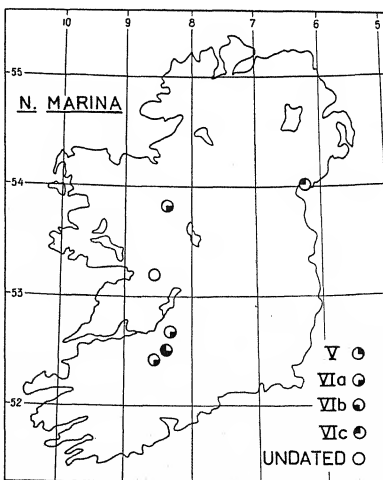


Fig. 2. Localities for *Naias marina* in Ireland.

Locality	Authority	<i>N. flexilis</i>	<i>N. marina</i>	Zone	Deposit	<i>Cereza</i>	<i>Cladium</i>	<i>Eleocharis</i>	<i>Mengianthes</i>	<i>Myriophyllum</i>	<i>Nymphaea</i>	<i>Phragmites</i>	<i>Potamogeton</i>	<i>Ranunc. aquat.</i>	<i>Ruppia</i>	<i>Scirpus</i>
Limerick																
Boskill.....	M.	+	+	VIa-c	Algal-mud		+						+			
Lough Gur.....	C.R.		+		Chara-mud											
Lough Gur.....	M.	+	+	VIa	Algal-mud		+									
Mountshannon.....	M.	+	+	VIa	Algal-mud	+	+									
Galway																
South-east.....	E.M.R.		+													
Roundstone II.....	K.J.	+		V-VIc	Detrit-mud	+	+	+		+	+		+			
Roscommon																
Carrowreagh.....	K.J.		+	VIa	Chalk-mud		+				+					
Louth																
Jenkinstown.....	M.	+	+	VIc	Algal-mud	+					+		+	+	+	+
Tyrone																
Baronscourt.....	M.	+		VIa-b	Algal-mud						+	+	+			
Antrim																
Cloughmills.....	K.J.	+		V	Algal-mud		+	+	+	+	+		+	+		+
Londonderry																
Newferry.....	K.J.	+		VIc	Fen-peat	+	+					+	+			

mud; one find of *N. flexilis* came from detritus-mud and one from fen-peat. The table shows the associated plant finds; remains of *Naias* were most frequently associated with *Cladium*, *Nymphaea* and *Potamogeton*.

All the dated fossil finds both of *N. flexilis* and *N. marina* belong to the Boreal period which Professor JESSEN (1) has divided into four stages in Ireland. In Zone V *Corylus* makes its first appearance; in Zone VIa it reaches its greatest values, in Zone VIb it falls back, and in Zone VIc it reaches a minimum

at the opening of the Atlantic period. *Naias* has not been found in inter-glacial deposits in Ireland.

The identifications were made by the author (M.), Professor KNUD JESSEN (K. J.), Mrs. E. M. REID (E. M. R.) and the late CLEMENT REID (C. R.) (2). The paper is offered as a supplement to the works of Dr. SANDEGREN (3) and Dr. BACKMAN (4).

¹ JESSEN, K., Proc. Roy. Ir. Acad., LII, B, 6, 1949.

² REID, C., Ir. Nat., XIII, 1904.

³ SANDEGREN, R., Sv. Bot. Tidskr., XIV, 1920.

⁴ BACKMAN, A. L., Acta Bot. Fenn., XLIV, 1948.

SESSION 7

July 18th, 2—5 p. m.

Chairmen: R. NORDHAGEN, R. S. ADAMSON and C. TROLL, Recorders: G. E. DU RIETZ and H. SJÖRS

SUBJECT:

Climate and Vegetation

C. G. G. J. VAN STEENIS (Bogor)
On the Hierarchy of Environmental Factors
in Plant Ecology¹

The elaboration of the second volume of the Flora Malesiana, which will comprise an account

of the vegetation types and their principal constituents in the Malaysian area, makes it desirable to explain the principles upon which my earlier, Dutch-written concise "sketches" of the vegetation of Malaysia (1935) were based.

¹ Read by H. C. D. DE WIT.

The study of a tropical region of great size has led me inevitably to consider its vegetation types from a broader basis than is generally done in local work in temperate countries. As a rule the analysis of plant communities has been based primarily on those of the temperate and cold zones of the globe, which are almost always in various degrees influenced by man and his domesticated animals. Besides, they are poor in specific composition, if compared with tropical forests, on account of the selection by macroclimatic factors which gain in severity with latitude.

This second volume of the Flora Malesiana, of which this first series of "Sketches" was a precursor, will be an account of the different vegetation types of Malaysia, based on literature, other information, and personal experience, while the manner in which they originated, how they shift, and for which reasons, how they are related mutually, and how they differ will be indicated. Besides, it will be attempted to define the predominant species and their associates, to co-ordinate the types with climate and soil, with dispersal, and with other factors of a historical character or belonging to the CEB-complexes, and to classify them tentatively according to natural or anthropogenic factors.

In 1935 my classification was mostly confined to a utilitarian, semi-artificial outline and enumeration of the types, and I abstained from an ample discussion as my space was limited.

One of the major problems in drafting a natural system of vegetation types is the hierarchy of the external factors.

WARMING, in 1895, mainly focussed attention on edaphical conditions; a few years later SCHIMMER accepted the climate as the main factor governing the vegetation types.

Climate and edaphical conditions are essentially below the level of the third one, *viz.* the historical factor. The latter determines the specific composition of the communities. First of all it is to be asked which species are available in a certain place of the globe. This initial historical factor is of course indisputably the highest in hierarchy. There is for instance no

question whether *Nothofagus* forests are climaxal for the Faroes simply because *Nothofagus* does not occur in the northern hemisphere. Nor is there any question of *Dipterocarpaceae* being dominant in the Amazon basin. The species composition of the vegetation types is, therefore, primarily governed by the historical factor. If the plant cover be imagined as a carpet, the historical factor is decisive for the texture.

There remains to be considered the importance of the set of climatic and that of edaphical factors. It seems to me that the only criterion for their sequence in the natural system of vegetation types is the degree of uniformity of their occurrence, *i. e.* the surfaces or areas in which they are uniform. The same principle should be applied in putting order to the minor factors which can be distinguished within the sets of climatic and edaphical conditions respectively.

If a region of 500 by 100 miles possesses a uniform, tropical "everwet" climate, it is evident that the edaphical factors finally determine the local types of vegetation. It might be suggested that these local types are edaphical "variants" of the climax vegetation, belonging to that particular climate. However, the botanical composition of the local types is often so widely different that the term "variant" is senseless in this respect: swamp forest and adjoining dryland forest have hardly any species in common. Ultimately, the local types, under uniform climatic conditions, are edaphical climaxes, climax understood as the stable natural vegetation under exclusion of anthropogenic influences.

If, however, a similar surface could be imagined with uniform edaphical conditions (incl. topography) but with a varied macroclimate, the botanical carpet would possess an edaphical ground, with a climatic pattern causing the variation, leading to climatic climaxes ultimately.

As far as my experience goes in Malaysia, the climate is far more uniform over large areas than are the edaphical (geological, pedological, and topographical) conditions. Therefore, the

climate should be placed higher in the hierarchy than the edaphical conditions, and, generally speaking, the climatic factors in this region determine the ground texture of the carpet, whereas the edaphical factors delineate the pattern.

Among the climatic factors are two main points: the distribution of rain throughout the year, and the temperature. In Malaysia both are regional, and the reason for placing the distribution of rainfall before the temperature is the essentially different botanical composition of seasonal or monsoon-forest vegetation prevailing under so-called semi-arid (or sub-humid) conditions if compared with the rain-forest, and further the fact that a monsoon forest is a one-storey forest in contrast with a tropical rain-forest, which is, except at high altitudes, at least composed of two storeys.

Regarding the set of edaphical factors, it can be said that this complex is far more varied than the climatic one. In Malaysia one of the most essential characters of the soil in relation to the forest type is the amount of water in or on the soil. There is a sharp distinction between so-called "dryland" forests and forests which are temporarily or permanently submerged (by fresh water). The latter cover enormous surfaces in Sumatra, the Malay Peninsula, Borneo, and New Guinea, and they possess a special botanical composition. There are several subtypes to be distinguished, *viz.* forests, which are flooded only part of the year, forests which are flooded permanently but without accumulation of peat, and forests which are flooded permanently with accumulation of peat (peat forests with black rivers). The flooded ombrogenous forests occur more or less regionally, and the factor 'water' occupies, therefore, a position superior to that of other edaphical factors.

The next category is that of "other soil conditions" which may occur more or less regionally, such as limestone, sandy soils, *etc.* They have priority above topographical factors, which occur at random and form the finest part of the pattern of climaxes.

It has sometimes been claimed that a climax formation is only the formation which occurs

in a certain spot under "mature" or "average" or "normal" conditions, which are governed exclusively by climatic factors. The promoters of this opinion reject the idea that there is a variation of soils due to local geology and topography; they maintain that all soils, under similar climatic conditions, will in the end reach the same composition under the prevailing climate and that, therefore, ultimately any plant formation will be a climatic climax.

Pedologists told me that this view regarding the soil is, even theoretically, hardly correct. The building of such a hypothetical uniform "climatic average soil", let us say in Borneo, from sandstone layers, from limestone, or from shales, would demand immense periods of time. The idea of such "climatic, uniform, average soils" is of no use for any practical plant ecology. Nature offers variation in soils, there is no "average" soil.

We know from geological records that the large primary tropical swamp forests have existed for ages, and as long as topographical conditions will remain as they are, these mature forests will keep their botanical composition. They are stable and there is no sense in talking about the type of forest which might replace the swamp forest, if there were no swampy depression but instead a hypothetical deep-profiled, level, dry climatic soil in the same spot. The same can be said about the mangrove: admittedly if there were no salt water, if there were no daily inundations, *etc.*, there would be a mixed dryland rain-forest. But the sense of such hypothetical considerations seems problematic.

In my opinion it is justified to define all stable non-anthropogenic formations as climaxes. In last instance all climaxes are edaphical.

Man has, through the ages, to a greater or lesser extent attacked the vegetation of Malaysia, and there is every reason to assume that man has been present in Malaysia since the time of the *Pithecanthropus erectus*. On the other hand, it is probable that only during the past few hundred thousands of years man influenced Malaysian vegetation to a high degree, ever since human civilization reached the stage

of the tending of cattle and the cultivation of crops.

The lofty rain-forest to which primitive, tropical man belonged, has always been and is still a great obstacle for the progress and development of civilization. As a matter of fact man never conquered that great nucleus of wet forests in West Malaysia and in New Guinea. Nevertheless, since the time that the indigenous tribes became acquainted with the use of fire, the destruction of the forests acquired greater dimensions.

It is natural that the influence of man was most destructive where the resistance of the forests and their natural ability for regeneration was weak, viz. in the forests of those regions which are subject to a yearly dry period (monsoon). In the monsoon forest the dry vegetable pile lies ready every year; hunting, cattle-breeding, and warfare, were and are the main stimulants which caused its regularly recurring inflammation. In Malaysia these periodically dry regions occupy the greater part of Central and East Java, many parts of the Lesser Sunda Islands, the southern parts of Celebes, the western parts of most Philippine Islands, and many parts of South New Guinea. Here prehistoric cattle-breeding tribes had their home. And I suppose that the extensive grass-lands and savannahs found in these areas date from ancient time.

It is sometimes assumed that large surfaces of deforested land owe their origin to former dense populations, but in my opinion this is only true in those cases where deforestation was due to a decline of an agricultural civilization and a subsequent abandoning of the fields. As a matter of fact there is, in Malaysia, no relation between the degree of deforestation and the present population density, but there is no doubt that deforestation is due to man.

With the introduction of agriculture, fields had to be cleared by means of axe and fire for the planting of millet and "dryland" rice. But the fields in the everwet forest-clad areas are easily overgrown by secondary growth, and, moreover, cannot be used permanently be-

cause the leached soils in the everwet tropics¹ are too poor for permanent cultivation. It is wrong to suppose that the West Malaysian and New Guinean forests have a rich soil; pedologically these soils are generally poor. This permits only a very rare use of the land (occupation once in 8-20 years) and resulted in the so-called "ladang" or shifting system of agriculture, a system which is still in use in many parts.

Permanent fields were introduced mainly with the cultivation of rice ("sawahs" or undated rice-fields), by which the everwet forest is definitely conquered. This wet-rice culture is, in Malaysia, as far as we know, not very old, and is supposed to have been introduced in our era under Hindu influence, though ethnographers place the introduction of the rice plant at a much earlier date. These permanent fields of a grain superior to millet have given rise to an increase of the original population.

This scant exposition may serve as an introduction to the consideration of the vegetation types resulting from deforestation. The analysis of these various types puts before us a large complex of many variable factors, causing vegetation types of various degrees of degradation and disintegration; and there are also the initial phases of regrowth. In every individual case it is important to know which destructive factors have been acting, and whether they are still active.

In practically all cases it can be safely assumed that the mixed forest is the original plant cover of Malaysia. The life-form and lifetime of the species dominating in wholly or partly destroyed forest types are of intrinsic value. There is for instance no doubt that *Pinus merkusii* originally was confined to local stations (landslides, mudstreams and other fresh volcanic soils, stony ridges) in the mixed North Sumatran forest, but that it later occupied all grounds burned or abandoned by man, as a pioneer weed. There is equally no doubt that these *Pinus* stands, left to themselves, will in the end be replaced by the mixed forest which penetrates

¹ In contradistinction to tropical soils under semi-arid conditions, and where soils are rejuvenated by volcanism.

gradually and prevents by its shade rejuvenation of the pine. But the lofty pines, once weeds, will tower over the mixed forest for centuries to come.

A much shorter period is needed for the restoration of a small clearing in the forest which is abandoned after one crop: a thicket is found the next year, a secondary forest of "weed trees" within 10 years, and (if not tilled in the meantime) after 50 years even a botanist will find hardly any trace of the former existence of a clearing.

An important detail in the recovery of the vegetation is the presence, or absence, of diaspores of the original vegetation, in other words: the presence of seed trees suitable for the rejuvenation of the original forest components. This is especially of importance for many large trees of the lofty forest. A large number of Malaysian forest trees have seeds which lose very soon their germinative power. In extensive deforested areas the transportation factor retards seriously the return of the original forest vegetation; primarily seral vegetation types will pioneer in these areas. Often it seems that the accidental occurrence of some seed trees may give rise to a local seral type (aggregate of a dominant). This is one of the reasons that different seres often grow to the exclusion of each other in a mosaic pattern. If we assume for instance that the really extensive grass-lands of Sumba Island, covering several thousands of sq. km, were no longer yearly burned, grazed, etc., these grass-lands would get quite a number of local seral growths, park-lands and savannahs, dependent on accidental seed trees and local opportunity for appearance as pioneers. But it would take ages in Sumba before these serals would have shifted to such an extent that closed mixed forest would have been formed similar in composition to the original monsoon-forest climax.

The complex of secondary growths and secondary forests is further connected with climaxes of various types of forest which do not represent succession stages in the strict sense, but which are due to factors of selection by

which certain species gain dominance. Teak forest for instance is (besides being planted in pure stands) a type derived from the mixed monsoon forest either by selective cutting or selection by ground fires through which teak gradually increases in numbers. In the same way most savannah types in the semi-arid areas are stands selected on fire resistance. In the mixed rain-forest such shifts can be observed also; in West Javan hill forest selected cutting of *Altingia excelsa* can lead to a (temporary) predominance of *Castanopsis* spp., filling the gaps made by the fellings. Seedlings of *Altingia*, in the substage, will gradually overgrow the *Castanopsis* canopy, but this process will require at least one hundred years.

These examples show that all intergradations between temporary and semi-permanent, and eventually subpermanent, anthropogenic vegetation types are present and that their status, respectively the direction in which they move along the stages of succession towards a restoration of the climax, is wholly dependent on local circumstances: this direction may be retrogressive (towards further deforestation) or progressive (towards accumulation of arboreal growth). They can be all classed under the heading "seres", if we keep in mind that CLEMENTS with this term denoted each series of temporary plant communities (series of succession stages) independent of the period of their existence. The term *sere* is then a very general term including both semi-permanent (ancient) degraded types (as are the steppes of Sumba and Timor) and types of very short duration (forest clearings).

After careful consideration I have refrained from drawing up a scheme and intricate terminology for the very numerous different cases which are known to occur. I will indicate the types by the names of dominating species, discuss the circumstances of their origin and of their future as far as seems justified and give an idea about the period during which they may persist.

One of the additional reasons for this is the fact that parallel to the series of seres due to

Concise Frame of a Natural System of
arranged according to the hierarchy of factors to which

Historical	Climatic		Edaphical	
Geographical position on the globe	Distribution of rainfall over the year	Temperature	Amount of water	Other soil conditions
Species available	Rather equally distributed over the year (everwet or feebly seasonal)	Hot to cool, up to $\pm 3\ 000\ m$	Temporarily or permanently submerged	<ul style="list-style-type: none"> Salt, sandy Salt, muddy Freshwater Peatwater Freshwater Coastal Sandy, inland Limestone
			Dryland	Other soils
Species available		Above $\pm 3\ 000\ m$
		Above $\pm 4\ 200\ m$
Species available	Semi-arid or seasonal, i.e. with a pronounced dry period	(not or scarcely present at high altitudes)
		

Climax Vegetation Types of Malaysia

they are due, including the serals belonging to them.

Edaphical Topographical conditions	Names of climaxes	Derived seral vegetation types ¹	
		Sample names of seres	Cause of seres
Submerged	<i>Sea-grasses & Algae</i>	?	Upsilting, eruptions, change of coast
Tides	<i>Mangroves</i>	Mangrove thicket seres	Total or partial cutting, drainage, agriculture
Inundated, no peat	<i>Swamp forests</i>	Swampy grassland seres	Drainage, cutting, burning
Same, peat present	<i>Peat forests</i>	Weed seres	Drainage, cutting, agriculture
Stagnant, deep	<i>Hydrophytes</i>	Shrub seres	Drainage
Swift running	<i>Rheophytes</i>	Grass and shrub seres	Silting by changed riverbed
Sandy & rocky	<i>Beach formations</i>	Grass, fern & shrub seres	Devastation, agriculture
Flat	<i>Myrtaceous forests</i>	Padang shrub	Devastation, burning, mining
Steep, rocky	<i>Limestone forests</i>	Shruberies, grass	Devastation, agriculture
Flat or sloping	<i>Rainforests</i> (mixed primary dryland forests)	<i>Natural seres:</i> Ridge forest seres Rock seres Mudwell seres Riverbank seres Landslide seres Hotwell seres Crater seres Lavastream seres Lahar (mudstream) seres Fumarole seres Wind seres Volcanic ash seres, etc.	Exposed, rocky, poor soil Exposed, rocky, very poor soil Mud-covering, often brackish Shifting soil on slopes High temperature, often brackish Hot, poison gas, sulphur Exposed, hot, soil absent Fresh mud-covering High temp. and moist air Devastation by gales Volcanism
		<i>Anthropogenic seres:</i> Shrub seres Fern seres Thicket seres Grass seres Field seres Reafforestation seres "Plenter"-forest seres Fire seres, etc.	Devastation, grazing Devastation, grazing, etc. Secondary growth succession Grazing, burning Abandoned fields & clearings Forest plantings Selected devastation Burning practice
.....	<i>Mountain scrub</i> (low, crooked forest)	<i>Natural seres:</i> Ridge seres Rock seres Landslide seres Crater seres Talus seres, etc.	Exposed, acid, poor soil Rocky, very poor soil Shifting soil on slopes Heat, poison gas, sulphur Shifting lapilli & rocks
.....	<i>Alpine vegetation</i> (low heaths & grassland)	<i>Anthropogenic seres:</i> Shrub seres Grass seres Fern seres	Devastation, grazing Burning practice mostly Burning and grazing
.....	<i>Monsoon forests</i> (mixed)	<i>Natural seres:</i> Salt seres (asinan) Rock seres Mudwell seres Riverbank seres Landslide seres Crater seres Lavastream seres Lahar (mudstream) seres Wind seres	Capillary salt through strong evaporation in dry season Rocky, very poor soil Mud-covering, mostly brackish Shifting soil on slopes Shifting soil on slopes Volcanism Exposed, soil nearly absent Covering with mud, hot or cold Devastation by wind
		<i>Anthropogenic seres:</i> Shrub seres Grass seres Field seres Reafforestation seres "Plenter"-forest seres Fire seres Savannah seres	Devastation, cattle grazing Abandoned fields, burning Abandoned fields, clearings Forest plantings Selected devastation Burning practice Burning, grazing

¹ Fern, grass and shrub seres all tend to succession stages towards the young secondary forest, and this to old secondary forest. The same holds for field and thicket seres.

anthropogenic influence there is a series of natural seres, caused by disturbing factors derived from Nature itself. *Albizia lophantha* may form pure groves in East Java after repeated fires in the mountain forest, but it forms also pure groves near some craters. *Pinus merkusii*, in North Sumatra, follows the footstep of man, but it equally pioneers abundantly on the big mudstreams of Tèlong Volcano and on landslides. The same can be said about *Casuarina junghuhniana* in East Javan mountains.

One of the striking features of the study of seral growths is the increase in numbers of certain species which originally must have occurred in limited numbers.

Of part of these species this behaviour could have been expected as they are of rather small size, light-loving (rejuvenate only in open spots), and pioneer as nomads in all places where the forest has been recently degraded (many *Euphorbiaceae*, *Urticaceae*, *Ulmaceae*, *Verbenaceae*). Some members of this group have been introduced but others are native to the Malaysian flora. The question arises where they found their natural habitat before the interference of man. Their niches, I believe, are found in the natural seres, such as along river banks, on landslides, on mudstreams, lake banks, rocks, talus, clearings made by wind, etc. As these local niches are mostly covering small surfaces, these secondary-growth species must have been rather rare originally. Their wide tolerance capacity, and their pioneer qualities, gave them an opportunity to multiply thousandfold and disperse widely when the forests were opened. These are cases similar to that of *Calluna* on the European heaths.

Among these pioneers, however, several species belong to the tall forest. It is strange to find forest trees such as *Schima noronhai*, *Engelhardtia serrata*, *Astronia spectabilis*, *Weinmannia blumei*, *Leptospermum flavescens*, etc. acting as pioneers on open soils, flowering and fruiting at an early age, and germinating in the light, when one is acquainted with these trees as common species in the forest, where they

rejuvenate in the shade. One would never have suspected trees of the everwet forest to possess such wide ecological tolerance capacities.

An important difficulty of defining and naming forest types is due to the storeyed forest vegetation. I agree entirely with the view now currently accepted that the highest closed level (canopy) is decisive for the composition, and not the emergent trees. Thus savannahs are essentially grass-lands with emergent trees. In defining types of the mixed forest this principle conceals practical difficulties, because the figures are mostly derived from sample plots of foresters, and to forestry the cubic content of the emergent giants of the forest is more important than the numbers of smaller trees of the closed canopy.

Another problem arises in field work when having to judge whether a vegetation type is seral or not. There are two indicators for seres: mostly they have sharp borders and one or very few dominating species. If the borders are not coinciding with climatic or edaphic discontinuities, there is a good chance that the type is seral.

The above-mentioned considerations have led me when drafting a concise scheme for a natural system of vegetation types which is appended to this paper.

L. EMBERGER (Montpellier)

Nécessité d'une entente internationale pour la classification des climats en biogéographie

L'étude de la végétation se rattache à la géographie physique, celle de la flore est liée aux vicissitudes historiques et géologiques du globe et au développement phylétique propre du monde végétal (paléobotanique).

Le milieu est le facteur qui règle la végétation. Milieu et végétation étant solidaires, il y a toujours, dans un même milieu, une végétation identique c. à d. biologiquement équivalente, la composition floristique pouvant être très différente (Exemple: Flores du Cap et de la Californie).

Les milieux fournissant les critères permettant

de faire les comparaisons phytogéographiques rationnelles, il est nécessaire d'avoir une connaissance aussi précise que possible des milieux, c. à d. avant tous des climats.

Malheureusement, aucune des classifications actuelles des climats ne donne satisfaction au phytogéographe; on constate même que la plus grande imprécision règne au sujet de notions qui, en apparence, paraissent cependant bien définies (Exemple, la notion de désert). Le défaut principal de toutes les classifications dressées à ce jour est qu'elles désirent être absolues c. à d. satisfaisantes pour toutes les disciplines. Or, une telle classification est impossible, les points de vue et les nécessités des diverses sciences étant trop divers et également légitimes.

Il y a donc plusieurs manières de classer les climats; chaque classification doit être faite en vue de la discipline qu'elle doit seconder. Les phytogéographes doivent donc avoir la leur, et celle-ci ne peut être que statique.

L'auteur propose que soit recherché un accord international sur ces importantes questions de principe et en indique les grandes lignes.

Schéma de classification des climats en phytogéographie.

A1. Climats non désertiques.

B1. Climats comportant une succession régulière de nuit et de jour.

C1. Climats intertropicaux.

D1. Climats isothermes sans saison sèche: Climats équatoriaux humides.

D2. Climats isothermes avec une saison sèche: Climats équatoriaux secs.

D3. Climats à saisons thermiques faiblement différenciées et pluies pendant la saison chaude: Climats tropicaux.

C2. Climats extratropicaux.

D1. Climats à saison sèche estivale: Climats méditerranéens.

D2. Climats à saison sèche hivernale: Climats extratropicaux dits continentaux.

D3. Climats sans saison sèche: Climats extratropicaux dits océaniques.

B2. Climats du «soleil de minuit».

C1. Climats subarctiques.

C2. Climats arctiques.

A2. Climats désertiques.

Discussion

G. E. DU RIETZ: In einem pflanzengeographischen System der Klimatypen sollte die Frostwintergrenze nicht vergessen werden. Diese Grenze teilt die „climats extratropicaux“ EMBERGERS in zwei Haupttypen, die eine mit Wintern mild genug, um eine Vegetation mit immergrünen Laubbäumen zu ermöglichen (EMBERGERS „climats méditerranéens“ und Teile seiner „climats extratropicaux dits océaniques“), die andere mit so strengen Frostwintern, dass die immergrüne Baumvegetation nur aus Nadelbäumen bestehen kann (EMBERGERS „climats extratropicaux dits continentaux“ und Teile seiner „climats extratropicaux dits océaniques“).

H. GESLIN souhaite que le vœu en discussion, avec tous documents complémentaires utiles, soit transmis à l'organisation météorologique Internationale dont le siège est à Lausanne. Cette organisation, qui réunit les chefs de tous les services météorologiques du globe comprend une commission de climatologie chargée notamment d'établir les bases d'une classification rationnelle des climats.

H. GAMS: Zur Winterfrostgrenze: Neue ausführliche Arbeit mit Karten von HERMANN VON WISSMANN 1950.

L. EMBERGER also took part in the discussion. He presented the following proposition:

«La Section de phytogéographes du 7^e Congrès International émet le vœu que la résolution, votée en 1935 à Amsterdam, de rechercher une entente internationale pour la classification et la définition phytogéographique des climats soit confirmée. Elle charge le comité créé à Amsterdam de reprendre les travaux en vue d'atteindre le but visé. Les résultats seraient soumis pour discussion au prochain congrès international.

La commission serait rattachée, comme sous-commission, à la commission d'Ecologie et géo-

graphie botanique, créé à Cambridge, appartenant à la section botanique de l'Union internationale des Sciences biologiques.»

This proposition was accepted unanimously by the Section and by the Third Plenary Session.

C. TROLL (BONN)

Die thermischen Klimatypen und das Vegetationsprofil der Erde

Die auf Zahlenwerte gegründeten Klimaklassifikationen, wie sie zuerst W. KÖPPEN und später C. W. THORNTWHAITE aufgestellt haben, reichen trotz ihrer starken Differenzierung nicht aus für die Vielfalt der physiographischen Erscheinungen auf der Erde, vor allem nicht für die Verhältnisse der Gebirge und für die gemässigten Klimate der Südhalbkugel. Eine ganze Reihe ökologisch höchst wirksamer Klimamerkmale und Klimaunterschiede werden damit nicht erfasst.

Eine erste Verbesserung wurde vom Autor angebahnt durch eine Charakterisierung der thermischen Klimate der Erde nach dem jahreszeitlichen und tageszeitlichen Gang der Temperatur, was durch die Darstellung in sog. Thermoisoplethen-Diagrammen deutlich wird (C. TROLL, Thermische Klimatypen der Erde. Petermanns Mitteil. 1943). Dabei erscheinen die Klimate der verschiedenen Breitenlagen in bestimmten Kurvenbildern und zwar die tropischen Klimate einschliesslich der Gebirge als ausgesprochene Tageszeitenklimate, die polaren als Jahreszeitenklimate, die der Mittelgürtel als Tages- und Jahreszeitenklimate. Die ökologisch besonders wichtigen Frostklimate wurden nach der Häufigkeit und jahreszeitlichen Verteilung der Frostwechseltage, Eistage und frostfreien Tage einer besonderen Untersuchung unterworfen (C. TROLL, Die Frostwechselhäufigkeit in den Luft- und Bodenklimaten der Erde. Meteorol. Ztschr. 1943). Ein für die Vegetationskunde wichtiges Ergebnis war es, dass die durch den geringen Landanteil bedingten ozeanischen bis hochozeanischen Klimate der gemässigten und subpolaren Breiten der Südhemisphäre bzgl. ihres Frostklimas eine grosse Ähnlichkeit

mit den Klimaten der tropischen Gebirge gleicher Mitteltemperatur aufweisen. An den morphologischen Wirkungen des Bodenfrostes (Tageszeitengefornnis gegenüber der vorherrschenden Jahreszeitengefornnis der Nordhalbkugel) kommt dies zum Ausdruck (C. TROLL, Strukturböden, Solifluktion und Frostklimate der Erde. Geol. Rundschau 34, 1944).

Die Erkenntnis führte zu der Entdeckung, dass auch eine sehr grosse Ähnlichkeit zwischen der Flora, den Lebensformen und den Vegetationsformationen der Subantarktis und der tropischen Hochgebirge besteht (C. TROLL, Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen auf der Nord- und Südhalbkugel. Jahresber. Geobotan. Forsch. Inst. Rübel in Zürich f. 1947, 1948). Florengographisch lässt sich dies im einzelnen aufzeigen an den zahlreichen Vertretern eines subantarktisch-andinen Florenelements (austral-antarktisches Florenelement TH. HERZOGS), einem subantarktisch-pazifisch-montanen Florenelement (Arbeiten von C. SKOTTSBERG) und einem von der Subantarktis bis in die Gebirge der andinen und pazifischen Tropen verbreiteten subantarktisch-tropischmontanen Florenelement.

Die pflanzlichen Lebensformen und Vegetationsformen in den beiden Regionen unterstreichen diese klimaökologische Verwandtschaft in erstaunlicher Weise. Es herrschen vor allem vier Lebensformen: 1. „Tussock“-Gräser verschiedener Gattungen; 2. Polsterpflanzen, besonders auch Hartpolsterpflanzen vom Typus *Azorella* und *Raoulia*, von denen nach W. RAUH etwa zwei Drittel aller bekannten Formen sich auf die Subantarktis und die Hochanden verteilen; 3. Wollige Kräuter (z. B. Konvergenz des andinen *Culcitium* und des subantarktischen *Pleurophyllum*); 4. Spalierteppich-Halbsträucher vom Typus *Acaena*. Dazu kommt, dass die Subantarktis auch ein Gegenstück zu den tropisch-montanen Stammschopfbblattgewächsen (*Espeletia*-Typ) in der endemischen Gattung *Pringlea* hat, wie auch die stammbildenden Arten der Farngattung *Blechnum* subgen. *Lomaria* sowohl auf den Inseln und Festländern der Subantarktis als auch in den tropischen Hochgebir-

gen auftreten. Ein bestimmter, an die frostwechselreichen Klimate der beiden Regionen gebundener neuartiger Moortypus ist das Hartpolstermoor (*Distichia-Moore* der tropischen Hochanden, *Donatia-Oreobolus-Moore* Neuseelands und Feuerlands).

Eine ebenso grosse Ähnlichkeit nach der systematischen Verwandtschaft (bis zur Artidentität) besteht zwischen den Nebelwäldern der tropischen Gebirge und den kühl-ozeanischen Regenwäldern der Südhemisphäre: *Weinmannia*, *Podocarpus*, *Drimys*, *Desfontainea*, *Embothrium*, *Nothofagus* (neuerdings auch in Neu-Guinea!), *Gunnera*, *Araliaceen*, *Fuchsia*, *Bambuseen*, *Cyatheaceen*, *Hymenophyllaceen* etc. Die Kugelschirmkronen vieler immergrüner Nebelwaldbäume der Tropen zeichnen auch die Bäume der antarktischen Waldgrenze (z. B. *Metrosideros lucida*) aus. Auch durch die Ornithophilie zahlreicher Gewächse und das Vorkommen der Blumenvögel (Honigvögel und Kolibris), die bis über die obere Waldgrenze der Tropen und bis an die antarktische Waldgrenze reichen (E. WERTH), wird die Ähnlichkeit der Klima- und Vegetationsbedingungen weiter unterstrichen.

Die Erkenntnis führt zu einer dreidimensionalen Zusammenschau der Naturerscheinung in einem Vegetationsprofil durch die Gebirge der Erde von der Arktis bis zur Antarktis (s. TROLL 1948). Schliesslich folgt daraus, dass für eine brauchbare Klimaklassifikation und eine verbesserte Darstellung des Pflanzenkleides der Erde diesen Tatsachen Rechnung getragen werden muss durch eine Zusammenschau von Vegetationskarten und Höhenprofilen der Vegetation.

Discussion

L. EMBERGER: Dans l'exposé de M. TROLL je distingue 3 chapitres principaux: l'un ayant trait à une question théorique d'étude des climats, l'autre comportant une comparaison entre la végétation antarctique et des hauts sommets des régions équatoriales, la 3^e sur la dissymétrie de la végétation du globe:

Je pense que l'importance du gel-dégel quo-

tidien est très grande, comme l'indique M. TROLL et quelle pourra être utilisée dans la séparation des diverses formes des grands climats qui se partagent le globe. L'alternance quotidienne diurne-nocturne du gel est sûrement un facteur important; je l'ai constaté dans le Grand Atlas, aux plus hautes altitudes.

La comparaison entre la végétation antarctique et celle des hautes montagnes équatoriales est justifiée.

En ce qui concerne la dissymétrie de la végétation des continents, je crois qu'il faut ne pas oublier l'histoire géologique du globe, que l'hémisphère Sud n'a pas été dévasté au quaternaire par des glaciations. Si la catastrophe quaternaire n'avait pas frappé l'hémisphère Nord, il est probable que la végétation y serait aussi luxuriante et diverse que sur l'hémisphère Sud.

P. W. RICHARDS: The mountains of Borneo, though north of the equator, have a vegetation which floristically and physiognomically is strikingly like that of New Zealand and Australia. The same appears to be true of the mountains in similar latitudes in South America. In Africa, on the other hand, there appears to be much less similarity between the vegetation of the tropical mountains and that of southern latitudes. Is there a less close similarity of climate in this case or is there some historical cause?

J. TROCHAIN: Il convient d'étendre l'importance des alternatives de gel et de dégel, dont il vient d'être parlé, aux oscillations de température le jour et la nuit.

En Afrique équatoriale c'est probablement au jeu de ce facteur que l'on doit d'observer des lichens épiphytes à de faibles altitudes, de l'ordre de 500 à 600 mètres, dans la région de Brazzaville, au cœur d'un pays de savanes arbustives, non primitives, très dégradées. L'existence de cette flore lichénique est ici anormale et ne peut s'expliquer par le simple jeu de l'humidité atmosphérique.

W. RAUH: Neben Klima spielt für Verbreitung der Polsterpflanzen auch Bauplan der Pflanzen eine Rolle.

H. MEUSEL: Die Deutung der Wuchsform der

Polsterpflanzen durch TROLL als Anpassung an das Frostwechselklima zeigt, dass die Wachstumsform nicht nur Ausdruck bestimmter Baupläne sondern auch Ausdruck bestimmter Umweltinflüsse ist.

C. TROLL: Das Fehlen antarktischer Florenelemente in den tropischen Gebirgen Afrikas hat keine ökologischen, sondern ausschliesslich genetische Ursachen. In Amerika und im Westpazifik bestehen junge Faltengebirgsgürtel von der Antarktis bis den Tropen (Grahamland — Antarkanden — Anden; New Zealand — Neukaledonien — New Guinea — Sunda); Afrika ist offenbar seit ältesten Zeiten weit getrennt. Allerdings sind auch die Hawaii-Inseln in ähnlicher Isolierung geblieben und die genetischen Zusammenhänge bleiben hier wie anderwärts (Cape — SW-Australia etc.) in Dunkel gehüllt.

Der Polsterwuchs ist auch nach meiner Meinung zunächst ein morphologisches Problem (RAUH). Aber die verschiedensten Familien und Genera, die die morphologische Anlage und Möglichkeit haben, können unter bestimmten ökologischen Bedingungen Polsterwuchs annehmen. Das Frostwechselreiche Klima der tropischen Gebirge und der Subantarktis ist dabei die wichtigste Möglichkeit. In Ostpatagonien ist bereits die Trockenheit mit im Spiele (*Mulinum* Dornpolster), ein zweites Konzentrationsgebiet sind die subtropischen Wüsten und Steppen, ein drittes die aussertropischen alpinen Hochgebirge. Die Kombination von thermischen und ariden Faktoren ist bei diesen verschiedenen „Polsterwuchs-Klimaten“ verschieden. Im übrigen möchte ich hoffen, dass sich bald Ökologen finden, die die extremen Vegetationsbedingungen in der Subantarktis (z.B. Kerguelen) und in tropischen Hochgebirgen (etwa im Anschluss an eine hochandine Minensiedlung) einer experimentellen Analyse unterziehen.

S. RIVAS GODAY (Madrid)

Essai sur les Climax dans la Péninsule Ibérique

La formation écologique-physiognomique (grand climax) la plus étendue sur la Péninsule

Ibérique est celle des *Durilignosa*, puisque le climat dominant auquel elle est soumise est méditerranéen. Les *Siccideserta*, indiqués par certains pour la Péninsule, ne sont pas climatiques; ce sont des états très dégradés du grand climax des *durilignosa*, d'origine édaphique-antropozoogène.

Suivent ensuite en importance les *Aestilignosa*, confinés dans le NO. N. et certaines zones montagneuses de la Péninsule.

Les *Aciculilignosa* sont modérément développées, peu étendues.

On peut établir les variantes suivantes de ces grands climax.

A.) *Durilignosa*. (Il appartient au *Cingulus Quercus ilicis* de SCHMID, à la Région du climax du *Quercion ilicis*.)

a₁) Variante thermique suave (elle est l'équivalent de l'étage méditerranéen tempéré d'EMBERGER).

a₂) Variante Ibéro-méditerranéenne intermédiaire.

a₃) Variante Ibéro-méditerranéenne froide. (Elle se ressemble en part à l'étage méditerranéen froid d'EMBERGER).

A/B) *Aesti-Durilignosa*: Climax mixte. (Intermédiaire entre deux climax; il appartient au *Cingulus Quercus roboris* et *Callunae*, *Quercus ilicis* et *Quercus pubescentis* de SCHMID; c'est-à-dire aux Régions du climax des alliances sociologiques du *Quercion roboris-sessiliflorae*, *Quercion ilicis*, et *Quercion pubescentis-sessiliflorae*; constitue en partie un étage ou degré de végétation indépendant du *Cingulus Quercus lusitanicae* et *Aceris monspessulani* RIVAS GODAY, proche de la Région de climax de l'alliance du *Pinion laricionis* de Corse, des *Quercetalia pubescentis* BRAUN-BLANQUET.) Elle est très polymorphe, ce qui correspond à son caractère mixte. Sur la Péninsule il peut être démembré en les suivantes variantes:

a/b₁) Variante océanique thermique. (Elle correspond à l'étage méditerranéen humide var. suave d'EMBERGER.)

a/b₂₋₃) Variantes subocéaniques thermiques sur sol siliceux et calcaire.

a/b₄₋₅) Variantes subcontinentales; sur sol

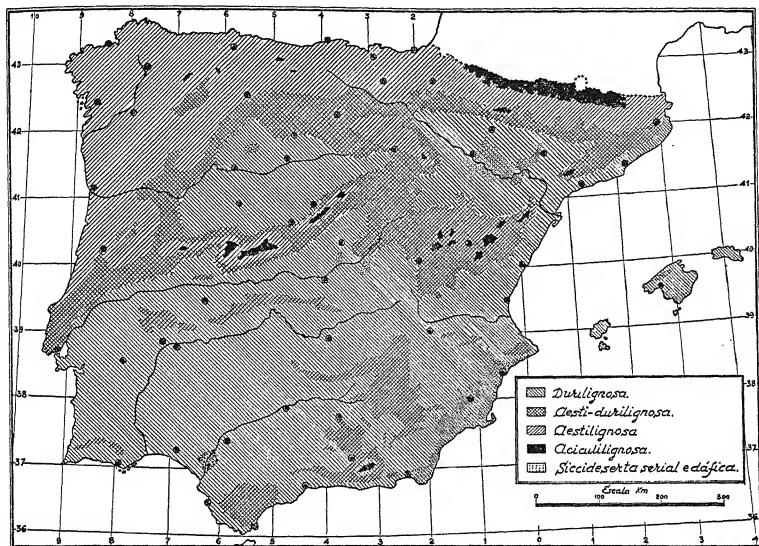


Fig. 1. Les Climax dans la Péninsule Ibérique.

de silice et calcaire. Les zones dégradées de montagne des variantes 3 et 4 sont l'origine de communautés ligneuses avec aspect de climax; sur sol calcaire, les *xeroacanthetae* de l'étage de haute montagne méditerranéen d'EMBERGER.

B.) *Aestilignosa*:

b₁) Variante océanique (correspond au *Cingulus Quercus roboris* et *Callunae* de SCHMID; c'est à dire, à la Région du climax du *Quercion roboris*; dans les états dégradés, il y a un faux climax d'*Ericifruticetae*, appartenant à l'alliance de l'*Ulicion*).

b₂) Variante subocéanique. (Appartenant au *Cingulus Fagi* et *Abietis*; c'est-à-dire, à la Région de climax du *Fagion silvaticae*.)

b₃) Variante subxérique avec influences méditerranéennes.

1) Sol calcaire avec hivers et étés modérés. (Elle représente le *Cingulus Quercus-Tiliae-Aceris* de SCHMID, mais avec *Tilia platyphyllos*.

On doit l'unir à l'alliance des *Quercion pubescentis-sessiliflorae*.)

2) Sol calcaire et climat plus extrême. (Elle représente le vrai *Cingulus Quercus pubescentis*, et appartient à la Région du *Quercion pubescentis-sessiliflorae*.)

3) Sol siliceux. (Même *Cingulus* que sous 2, mais à communautés acidophiles du *Quercion roboris-sessiliflorae*. Notre *Quercion roboris-tozzae* var. *pyrenaicae*.)

C) *Aciculignosa*:

c₁). Variante typique. Se présente seulement d'une manière isolée dans les Pyrénées; elle est conditionnée par le sol siliceux comme le *Rhodoreto-Vaccinion* (*Cingulus Laricis* et *Pinus Cembrae*).

c₂) Variantes finicoles pour influence méditerranéenne. La composition est différente selon la nature du sol: *Sarothamnus purgans* et *Juniperus nana* sur sols siliceux, et *Juniperus*

sabina, *humilis*, *Astragalus nevadensis*, etc., sur les calcaires.

Aspects alpinoides fréquents.

Discussion

H. GAUSSEN: Les forêts de *Pinus pinaster* du Portugal, celles de *P. pinea* et *pinaster* de Castille ne sont-elles pas des climax?

Il y a des *Durilignosa* aux Pyrénées dans tous les terrains.

D'autre part une partie des steppes que WILLKOMM avait distinguées provient de la dégradation de forêt de *Q. ilex*. Mais une partie sur sol salé est authentiquement steppique.

I. REICHERT: What is the climax vegetation of the steppes of the Iberian Peninsula? One cannot consider the steppe vegetation in Spain as degraded. It is natural and resembles that of North Africa. It is impossible to say, as the speaker, that *Quercus* is the climax of the steppes.

W. ROTHMALER: I. Die *Durilignosa* von RIVAS im engeren Form zerfallen in *Oleo-Ceratonion* nahe der Küste bis Südkatalonien, in *Quercetum ilicis galloprovincialis* in Katalonien, der übrige (innere) Teil der Halbinsel gehört zu *Quercus rotundifolia*-Gesellschaften, die auch die Steppen einschliessen.

II. In Griechenland wie in Spanien ist das *Oleo-Ceratonion* (après EMBERGER) gut von den anderen Hartlaubgesellschaften unterschieden, es umfasst echt mediterrane, küstennahe Teile im Süden beider Halbinseln.

E. SCHMID: Die Climax der südostspanischen Steppengebiete gehört zu den Steppen des *Stipa tortilis*-Gürtels und ist zu vergleichen mit den nordafrikanischen *Stipa tenacissima*-Steppen. Sie besitzt eine eigene Flora, was von dem „*Oleo-Ceratonion*“ nicht gesagt werden kann. Dieses letztere ist ein anthropogen sehr stark veränderter Teil des *Quercus ilex*-Gürtels mit zahlreichen Ingressionen aus ganz verschiedenen Gürtel-Typen.

M. ZOHARY: The *sicoideserta* with *Artemisia herba-alba* cannot be conceived otherwise than as secondary vegetation, because of the prevailing mediterranean climate.

L. EMBERGER: Je suis conduit à faire une observation au sujet de la remarque faite par M. SCHMID qui pense que l'*Oleo-Ceratonion* n'existe pas et représente un *Quercetum Ilicis* dégradé. Je pense, au contraire, que ce groupement existe et est parfaitement autonome, comme le montre l'ensemble de l'étude de l'*Oleo-Ceratonion* dont il existe de grandes surfaces depuis Agadir jusqu'à Tunis. Tous les phytogéographes de l'Afrique du Nord sont d'accord sur ce point.

S. RIVAS GODAY: La *sicoideserta* de la Península Ibérica es seral edáfica, en disclimax (CLEMENTS), no climática; siguiendo al español HUGUET DEL VILLAR.

La *Durilignosa*, es del grado de vegetación de *Quercus ilex* ó *Cingulus Quercus Ilicis* de SCHMID.

C. TROLL: Die Auffassungen über Klimax sind verschieden. Hier wurde ausschliesslich klimatische Klimax gemeint; von v. STEENTS wurden alle stabilen, nicht-anthropogenen Gesellschaften, also auch edaphisch bedingte, als Klimax aufgefasst.

J. TROCHAIN also took part in the discussion.

CH. SAUVAGE (Rabat)

Les reliques de la flore tropicale au Maroc

Ces dernières années ont amené la découverte de plusieurs plantes tropicales dans le Sud marocain et il était intéressant de se rendre compte de l'importance et la répartition de cette flore tropicale au Maroc. Pour le dépouillement systématique, j'ai considéré comme appartenant à la flore tropicale, les plantes qui dans la nomenclature de EIG sont rangées dans l'élément soudano-deccanien (Sd), le groupe de liaison soudano-deccanien sahare-sindien (Sd-Ss) et le groupe tropical des plantes plurirégionales (Prt).

Si l'on cartographie la répartition au Maroc de chacun de ces trois éléments ou groupes, aucune conclusion nouvelle ne ressort. On peut par contre établir les cartes suivantes:

1° Plantes du bord des eaux permanentes (8 espèces).

Elles peuvent s'abstraire plus facilement du rythme climatique. Une moitié appartient à l'élément Sd (ex.: *Sporobolus robustus*), l'autre moitié au groupe Prt (ex.: *Eclipta alba*). Leurs stations isolées montrent le caractère reliquaire, mais elles sont réparties surtout dans deux régions jouant un rôle de relais dans les migrations d'oiseaux: le Rharb et les grands oueds du Sud marocain.

2°/ Plantes des lieux plus secs et n'existant qu'en quelques stations (15 espèces). 7 espèces appartiennent à l'élément Sd (ex.: *Tephrosia leptostachya*, *Leptadenia pyrotechnica*) et sont très disjointes de leur aire principale. Le Zemmour forme un relais au Sahara occidental pour deux d'entre elles. Les 8 autres appartiennent au groupe Sd-Ss (ex.: *Balanites aegyptiaca*) avec, souvent, une préférence pour le domaine Sd. En général elles sont reliées à l'aire principale par des stations intermédiaires au Sahara occidental (en particulier Zemmour). Toutes les stations marocaines de ces 15 espèces sont enveloppées par une ligne qui, partant de Fouta Zguid, suit le flanc sud du Bani et se termine près de Goulimine à l'embouchure de l'O Asaka.

3°/ Plantes des lieux plus secs et à large répartition (19 espèces).

La plupart ont une aire de répartition bien équilibrée entre les régions Ss et Sd (ex.: *Andropogon schoenanthus*), quelques unes avec une préférence Sd (ex.: *Calotropis procera*). 12 d'entre elles ne dépassent vers le nord la limite du Bani.

Ainsi le Jebel Bani paraît dessiner une limite floristique très importante. Il constitue aussi

une limite climatique et il n'est pas interdit de penser que cette montagne a joué un rôle important de barrière, soit dans un sens, soit dans l'autre, pendant tout le Quaternaire.

Discussion

J. TROCHAIN: Parmi les plantes d'Afrique tropicale qui, au Maroc, sont localisées au bord des eaux permanentes et que, pour cette raison, M. SAUVAGE réunit dans son 1^{er} groupe, certaines (dont *Chloris gayana*, *Eclipta alba*, *Pluchea ovalis*, si j'ai bien saisi leur nom au passage) ne sont pas là dans leur station normale.

En effet, au sud du Sahara, en territoires sahélien et soudanien, ces plantes occupent, au contraire, des sols secs, sableux, plus ou moins arides. Il s'agit donc pour elles, au Maroc, de stations hétérotopiques.

Il serait intéressant de voir s'il ne s'agit pas, là, d'une nouvelle vérification de ce que j'ai avancé dans mon travail sur la végétation du Sénégal (Mémoires IFAN, N° 2, 1940), à savoir que des plantes qui normalement croissent, en région aride, sur de sols légers, sableux, exigent, lorsque l'humidité totale du milieu augmente (eau du sol, pluie et hygrométrie de l'air) un sol plus argileux, donc plus lourd. Il existerait en somme un balancement, une compensation, entre l'humidité de la station et la compacité de son sol, compacité qui entraîne des différences dans son pouvoir de rétention pour l'eau.

CH. SAUVAGE and L. EMBERGER also took part in the discussion.

SESSION 8

July 19th, 9 a. m. — 1 p. m.

Chairman: H. MEUSEL, Records: G. E. DU RIETZ and H. SJÖRS

SUBJECT:

Vegetation Units

J. BRAUN-BLANQUET (Montpellier)
Le classement des unités végétales

Les Unités de Végétation peuvent être classées d'après les principes suivants:

Physionomie, Ecologie, Chorologie (types de distribution), Syngénétique (développement), Affinité floristique.

Physionomie. La plus ancienne classification est celle qui repose sur l'aspect physionomique

des groupements: forêts, garrigues, prairies, landes, steppes etc., conceptions très générales empruntées au langage populaire et compris par tout le monde. Mais ces Unités sont trop peu précises pour servir de base à une classification scientifique.

Classification écologique. Cette classification se base ou sur les conditions stationnelles complexes et encore trop peu connues, ou bien sur la forme biologique des espèces considérée comme expression de l'ensemble des facteurs stationnels. Mais cette dernière présomption est-elle suffisamment justifiée?

Classification écologique-physionomique. Une combinaison entre les deux premiers modes de classement a été introduite par SCHIMPER 1898. Transformée et adaptée, cette classification écologique-physionomique peut rendre de bons services dans les pays peu connus où l'étude de la systématique des espèces est encore à ses débuts. C'est le cas de certains pays tropicaux.

Classification chorologique. Une classification basée sur la répartition des groupements végétaux n'est possible que pour des ensembles très vastes: étages altitudinaux, ceintures de végétation, cercles de groupements qui, eux-mêmes, comprennent déjà toute une hiérarchie d'unités phytosociologiques de valeur différente.

Classification dynamo-génétique. Ce classement gravite du tour du point crucial qu'est le climax climatique de la végétation. Or rien n'est plus discuté, ni plus difficile à établir que ce climax. Dans beaucoup de contrées il a disparu ou tend à disparaître. L'influence anthropozoiique gagne de plus en plus en importance, le développement de la végétation est de plus en plus influencé et dirigé par l'homme.

On peut facilement classer les successions, mais ce classement semble peu apte à servir de

point de départ pour une systématique générale fondée sur l'ensemble des groupements végétaux et leur subordination.

Classification floristique. Reste la classification d'après la composition floristique des groupements végétaux, la seule basée sur les objets concrets qu'il s'agit de classer, et non sur des caractères et considérations hors de ces objets, d'interprétation divergente et variable.

Chaque groupement végétal est un ensemble d'individus spécifiques, différents d'après leurs exigences stationnelles, leur répartition, leur importance dynamo-génétique et leur origine.

Chaque espèce ou unité systématique inférieure devient ainsi un indicateur précieux, écologique, chorologique, syngénétique etc.

Il s'agit donc d'abord de reconnaître les groupements floristiques typiques qui se rencontrent dans la nature, prendre autant de relevés que possibles des unités reconnues et les classer dans des tableaux d'associations ou sociations pour fixer et circonscrire leur individualité.

Comment ces groupements floristiques définis, associations ou sociations, peuvent-ils être classés?

Actuellement trois possibilités se présentent:

1° Le classement d'après les espèces dominantes,

2° Celui d'après le coefficient de communauté des espèces (Quotient of Similarity), faisant abstraction des considérations d'abondance, de dominance et de fidélité des espèces,

3° Le classement d'après la localisation sociologique, la fidélité.

Après avoir longtemps et minutieusement étudié et comparé ces trois possibilités, la troisième a été choisie et le système de subordination suivant a été proposé:

Cercle de groupement:			Exemples:
Classe:	terminaison	-etea	(<i>Quercetea ilicis</i>)
Ordre:	»	-etalia	(<i>Quercetalia ilicis</i>)
Alliance:	»	-ion	(<i>Quercion ilicis</i>)
Association:	»	-etum	(<i>Quercetum ilicis</i>)
sous-association:	»	-etosum	(<i>Quercetum ilicis pubescentetosum</i>)
Variante:	—	—	(<i>Quercetum ilicis pubesc.</i> variante à <i>Quercus coccifera</i>)
(Faciès):	—	—	(Faciès à <i>Carex humilis</i>)

Comments

added to the Chairman's thanks for the paper.

H. MEUSEL: Der Ausgang der Diskussion über Vegetationseinheiten ist die Forderung einer „naturgemässen Einteilung“ (BRAUN-BLANQUET). Frage ob eine solche naturgemässe Einteilung nicht in hohem Mass die Verteilung der Pflanzen und der Pflanzengesellschaften im Raum berücksichtigen muss und ob deshalb die vom Vortragenden vorgeschlagene Trennung von Pflanzensoziologie und Pflanzengeographie gerechtfertigt ist.

R. NORDHAGEN (Oslo)

Vegetational Units in the Mountain Area of Scandinavia

See:

NORDHAGEN, R., 1928: Die Vegetation und Flora des Sylenegebietes. — Skr. utg. av det norske videnskaps-akademi. 1. Matem.-Naturvid. klasse. No. 1. Oslo.

— 1936: Versuch einer neuen Einteilung der subalpinen-alpinen Vegetation Norwegens. — Bergens Museums Årbok 1936, Nat. vet. rekke Nr 7. Bergen.

— 1943: Sikilsdalen og Norges fjellbeiter. — Bergens Museums skrifter Nr 22. Bergen.

Comments

added to the Chairman's thanks for the paper.

H. MEUSEL: Wichtiger Beitrag zur Verständigung der nordeuropäischen Schule der Pflanzensoziologen. Übereinstimmung in der Auffassung über die Grundlagen der Vegetationsanalyse (Assoziationslisten mit gleichzeitiger Berücksichtigung der Charakterarten und der Konstanten).

Besonders beachtenswert ist, dass die höheren Vegetationseinheiten eine charakteristische Verteilung in der Landschaft zeigen und deshalb in Form von Karten und Profilen gut dargestellt werden können.

H. H. ALLAN (Wellington)

Classifying Vegetation for the Geographer

The attempts at a formula treatment of plant communities by KÜCHLER (1947), DANSEREAU

(1949), CHRISTIAN (1949) are based fundamentally on the structure of the vegetation, irrespective of floristic details. All three commence with a symbol for life-form. KÜCHLER has seven major symbols and four subordinate groups, involving in all 25 letters. A particular, not very complicated, type of N. Z. forest yields the formula BdcjshE. DANSEREAU's scheme also requires 25 letters. He adds 18 diagrams, each of which may be modified. The same piece of N. Z. forest requires the formula ThecELFHTn. Taking the structural element only in CHRISTIAN's scheme we arrive at AxEyLyBx-yCx-y, further modifiable by three grades of height. This forest, in general terms, is dominated by "broadleaf" evergreen trees, of continuous dense growth, with abundant epiphytes, conspicuous lianas and undergrowth of shrubs, and a floor cover of herbs other than grasses, with some "needle-leaf" evergreen trees present.

It is suggested (a) that adequately to express the plant-cover formula treatments become too complicated and lend themselves too easily to abuse; (b) that for a formula treatment to be generally acceptable it must be strictly limited and based on symbols taken from Latin rather than a modern language; (c) that a formula treatment is more likely to be of use for note-taking than for final treatment. RÜBEL's classification of the plant communities of the world (1936) might serve as a basis.

The matter should be further explored; it seems desirable that geographers in general, as well as phytogeographers and plant ecologists, should discuss together the problem involved.

Literature

CHRISTIAN, C. S., 1949: "The vegetation of the Berkeley Tableland." Paper read before the Hobart meeting of A.N.Z.A.A.S. Abstract.

DANSEREAU, P., 1949: "Structural units of vegetation in tropical and temperate climates with special references to Pacific area." Paper read before Seventh Pacific Science Congress, N.Z. Abstract.

KÜCHLER, A. W., 1947: "A geographic system of vegetation." *Geog. Rev.* 37 (2) 233—240.

RÜBEL, E., 1936: "Plant communities of the world." *Essays in Geobotany in Honor of William Albert Setchell*, 263—290. California.

E. SCHMID (Zürich)

Propositions for the Analyses of Vegetation

In biocoenology we notice today a tendency to intensify the analysis, to complete the data, for instance we work with full areas of species and related groups of them, and further we observe the tendency to synthesis. Our object is no entirety, it is like a landscape, like a geological formation. There are no individuals, and we cannot make classifications, only types. Assortment of species and assortment of representation types do not go parallel. Therefore we found the life-communities on the biological types and the main division of vegetation on the flora (vegetation belt).

We have to make three analyses:

The floristical analysis. The fundamental data are the individuals of plants and animals and the sum of their stations. In analysing we ascertain taxonomy, variability and relationships, phylogenetic and genetic position, distribution (areas) and the history of migration and we obtain by synthesis abstractively species, subspecies, varieties, areatypes, floristical types and finally the main division of the vegetation, the vegetation belt, which is built up by the flora and vegetation of a certain areatype.

The biological analysis. We start from the individuals' corpo-reality, from the individuals and their habitat. We analyse: axial system (systemaphor), light, temperature, humidity, nutrition, propagation, dissemination, special biological correlations, influence of man, environment (habitat) and we come, synthesizing, to the biological pattern of the type of representation, to the statistics of habitat.

The biocoenological analysis. The fundamental data are the individuals in the life-community. We analyse mapping squares of the vegetation, subdividing the squares in smaller ones. We notice the individuals in every square and their size and dominance. We make transects. We make statistics of the participation of our species in the biocoenoses where we find them. In the synthesis we obtain the species-area-curve, the representation type-

area-curve, the assortment of representation types, the spectra of the floristical and representation types, the pattern of the biocoenosis (secondary division of vegetation, regional and local biocoenoses).

The efficiency of the method in the floristical, phylogenetical, epiontological and biological directions is demonstrated by the example of numidian oakwoods.

The materials of biocoenology are increasing to such a degree that they begin to extend beyond our range of sight. So we are forced to consider simple and clear methods. But it is by no means necessary to produce in a hurry a premature statement of the vegetation. The work will need more than one generation and a method that is elastic enough to take up the additions of new knowledge and correction.

H. GAMS (Innsbruck)

The Importance of Growth Forms for Taxonomical and Ecological Systematics

From ARISTOTLE and THEOPHRASTOS to most botanists of the 16th century, plants were classed according to their growth or life forms. Since CESALPINO, JUNGUS, MORISON and others, these characters have been increasingly neglected in favour to those of the reproductive organs and accepted only for purely descriptive and ecological purposes, especially by HUMBOLDT, GRISEBACH, H. v. POST, KERNER, WARMING, and RAUNKIAER. The importance of life forms for the classification of vegetation units has been emphasized especially by SCHIMPER, WARMING, SCHRÖTER and many others as the only natural basis of a universal system of vegetation. Some "phytosociologists" have tried to abstract from life forms and to construct a system exclusively according to floristic affinities. Those tentatives fail by the simple fact that these affinities furnish a pluridimensional system and can be reduced to a more or less linear one only by artificial conventions without any scientific value or by introduction of a reasonable system of life forms. The necessity of separating errant, adnate and radicate communities is generally

recognized also by many defenders of purely floristic systems.

From MORISON and HUMBOLDT to RAUNKIAER and DU RUIZ, the first place among radicate life forms is assigned to the arborescent ones, RAUNKIAER's Phanerophytes. As RAUNKIAER's pupil MØLHOLM HANSEN (1930) has shown, this is in accordance with the fact that Phanerophytes have been absolutely dominant from the Carboniferous or upper Devonian to the Cretaceous. The actual dominance of dwarf shrubs and other Chamaephytes in certain regions around and beyond the timber lines and of Hemikryptophytes in others is a quite recent feature. Therophytes are certainly one of the youngest groups.

I venture to assert that the whole evolution from the Devonian Pteridophytes, not only to all Gymnosperms but also to the highest families of Angiosperms, has taken place among Phanerophytes. The Silurian and Devonian Psilophytes are certainly derived from more or less amphibic Hydrophytes, but all angiospermous and perhaps also bryophytic Hydrophytes are derived from terrestrial ancestors. *Nymphaeaceae* and *Helobiae* are descended from terrestrial, originally phanerophytic *Polycarpicae*, and it is most improbable that Palms and arborescent *Liliiflorae* should be derived for instance from *Helobiae*.

I cannot accept HUTCHINSON's division of Dicotyledons into predominantly arborescent and predominantly herbaceous families. With very few exceptions, as *Nymphaeaceae*, *Helobiae*, *Lemnaceae* and *Podostemonaceae*, all families contain Phanerophytes and these belong always to the oldest taxa up to the *Compositae* with the giant *Senecios* as the probably most primitive ones. It is therefore quite reasonable to range also the phanerophytic biocenoses (forests) before the chamaephytic (heaths) and the yet younger hemikryptophytic (meadows), geophytic and therophytic ones as the youngest.

Many errant and adnate life forms and especially the aquatic ones are certainly older than the radicans and their communities should be ranged before the *Phanerophytia*. Pleustic Sar-

gassums are derived from adnates, pleustic Bryophytes, Pteridophytes and Angiosperms from radicans. Only among the oldest Archegoniates (e.g. *Andreaea*, *Psilotum*), some may be primarily adnate. The majority of adnate Bryophytes, Pteridophytes and Angiosperms is certainly younger, e.g. among hepatics the *Jubuleae*, among mosses the *Isobryales* and among ferns the *Hymenophyllaceae*. Many of these and also lichens (many *Parmeliaceae*, *Stictaceae* etc.) grow both as Epipetria on rocks and as Epiphytes or Epixyles on trees. It is most probable that they have evolved as Epiphytes in tropical rain forests during the Mesophytic. No representatives of these relatively modern *Jungermanniales*, arthrodont mosses and leptosporangiate ferns are known from the Palaeophytic. Their epipetric communities are much poorer than the epiphytic ones and perhaps only of Quaternary age.

It seems not advisable to divide all adnate societies of algae, lichens and mosses into Epipetria and Epiphytia or Epixylia, but we must recognize an important group of primarily epiphytic, secondarily epipetric communities. Of the radicate moss communities, those of *Polytrichales*, *Dicranales* etc. are primary radicans; others, like those of *Amblystegiaceae* and *Hypnaceae*, according to M. FLEISCHER derived from adnate *Isobryales*, are secondary ones.

H. MEUSEL (Halle/S.)

Die Bedeutung der Wuchsformen für die Entwicklung des natürlichen Systems der Pflanzen und für das Verständnis der Pflanzengesellschaften

Während für die Entwicklung der Vegetationskunde die Wuchsformen immer eine gewisse Rolle spielten, wurden sie von den Systematikern meist nur wenig beachtet. Man betrachtete in der Regel nur die Konvergenzen im Vegetationsaufbau bei Pflanzen verschiedener systematischer Stellung und bezeichnete sie als Anpassungsmerkmale. Genauer besehen bestehen aber keine grundsätzlichen Unterschiede zwischen Anpassungs- und Organisationsmerk-

malen. Jedes Merkmal hat sowohl konstitutionellen als auch umweltsbedingten Charakter. Die Wuchsformen sind deshalb nicht allein Ausdruck einer Anpassung an bestimmte augenblicklich herrschende Umweltsverhältnisse sondern ebenso Ausdruck einer bestimmten im Laufe der Erdgeschichte entwickelten spezifischen Konstitution. Deshalb sind auch die Wuchsformen für die Entwicklung des natürlichen Systems bedeutsam. An Beispielen wurde gezeigt, wie bei Berücksichtigung des Gesamtbauplanes (der sich häufig in den Symmetrieverhältnissen ausdrückt), auch in der vegetativen Region der Pflanzen systematisch wichtige Merkmale gefunden werden können (Unterschiede in der Symmetrie des Vegetationskörpers bei den *Hepaticae* und *Musci*, charakteristische Wuchsformen der einzelnen natürlichen Sippen der *Musci*: *Polytrichales*-Form, *Isobryales*-Form, *Hypnales*-Form usw., Wuchsformen der Araceen und Lemnaceen).

In der Vegetationskunde wurden die Wuchsformen zunächst äusserlich beschreibend betrachtet (physiognomische Richtung HUMBOLDTS, GRISEBACHS u. a.). Später sah man in ihnen den Ausdruck bestimmter Umweltfaktoren (ökologische Richtung von RAUNKIAER und WARMING). Heute erscheinen uns die vergleichend morphologisch analysierten Wuchsformen vor allem bedeutsam zur Erkenntnis der Struktur der Pflanzengesellschaften. Hinweise auf die Gliederung des Wurzelraumes!

Die Wuchsformenbetrachtung ermöglicht

1. den Aufbau der Vegetation aus ihren einzelnen Komponenten klar zu umschreiben. Bildung von Synusien und Sociationen, Schichtung der Pflanzengesellschaften.

2. die räumlichen Beziehungen zwischen Pflanzenwelt und Umwelt übersichtlich herauszuarbeiten. Verteilung der Gewächse im Erd- und Luftraum.

Die Kenntnis dieser räumlichen Zusammenhänge ist Voraussetzung für jede soziologische und ökologische Analyse der Pflanzengesellschaften und liefert die Unterlagen für eine geographische Gliederung der Vegetation. Sind die Wuchsformen für die Entwicklung des na-

türlichen Systems insofern wichtig, als sie als Ausdruck bestimmter Sippenbaupläne anzusprechen sind, so ermöglicht die Wuchsformenbetrachtung in der Vegetationskunde eine natürliche geographische Gliederung der Pflanzengesellschaften, die ausgeht von der zonal-regionalen Anordnung der Vegetation auf der Erde, die die Aufgliederung der Vegetationsgürtel in natürliche Landschaften mit einem charakteristischen Mosaik von Formationen und Assoziationen untersucht und die schliesslich ausmündet in die Betrachtung der räumlichen Struktur der kleinsten Vegetationseinheiten.

Discussion

C. TROLL: Herr BRAUN-BLANQUET mit seinem besonders klaren Eröffnungsvortrag über seine pflanzensoziologischen Methoden und die übrigen Redner bis zu den Schlusssätzen des Vortrags von Herrn MEUSEL haben das Problem in voller Breite dargelegt. Dem floristisch-statistischen System BRAUN-BLANQUETS, das von den Assoziationen über die Verbände, Ordnungen und Klassen zu den Kreisen führt, kann ein ökologisch unterbautes räumlich-geographisches System gegenübergestellt werden, das umgekehrt bei den grossen klimatischen Vegetationsgürteln beginnt und über klimatische Vegetationsgebiete und edaphische Klimaxvereine zu den kleinsten Vegetationskomplexen führt. Die Profile NORDHAGENS z. B. haben diese räumliche Gliederung im kleinen gezeigt, die klimatische Grossgliederung wurde in anderen Sitzungen behandelt. So wie von NORDHAGEN von einer floristischen Melodie der Pflanzenvereine, so könnte auch von einer geographischen Melodie der Pflanzenvereine gesprochen werden. Letzten Endes würden diese Melodien zur Symphonie des gesamten Pflanzenkleides zusammenklingen.

R. NORDHAGEN: The floristic system contains much more than the pure "floristic" aspect of the thing. The tables enable us to "read" out facts about the ecology of the community (xerophilous, mesophilous etc.) because a great many plants are indicators of for instance dryness, soil mineral composition (lime or no lime), humidity of the atmosphere, etc.

There is no "natural system" of vegetational classification. The most "natural" system is the one which gives you the most important information about the units, their structure, ecology and distribution.

W. ROTHMALER: Wie BRAUN-BLANQUET überzeugend nachwies, ist das angestrebte ökologische System nicht realisierbar. Wie NORDHAGEN ausführte, enthält die floristische Ordnung gleichzeitig in ihren einzelnen Komponenten die Ökologie, Chorologie und Geschichte der Arten. So scheint es am besten auf diesem Wege zu einer Einigung in der Pflanzensoziologie auf floristischer Basis zu kommen. MEUSEL wies auf die Mischung von Lebensformen und Wuchsformen in jeder Gesellschaft hin und zeigte in seinen Wurzelhorizontuntersuchungen, dass die floristische Methode auf dem richtigen Wege ist.

Die Unterscheidung von Anpassungs- und Organisationsmerkmalen der Berliner Schule wird glücklicherweise nicht mehr aufrecht erhalten (z. B. JULIAN HUXLEY etc.), es sei dabei auf die jetzt anerkannten taxonomischen Beziehungen zwischen *Aizoaceae* und *Cactaceae* hingewiesen.

H. SJÖRS: Prof. NORDHAGEN has already pointed at the limitations of the systems of vegetation. As Prof. GAMS pointed out, the floristic and other affinities of plant communities offer a basis of systems that are essentially pluridimensional. Some simple cases may be successfully represented in a two- or three-dimensional coordinatic scheme, but often the directions of variation are too many to be visualized at the same time. The ordinary method of making vegetational systems involves that the directions of variations are considered in a certain order. The direction which seems to be the most important one may be used in separating the higher units, for instance the alliances, and directions which seem to be less significant may be used in separating the lower units, for instance associations or sociations. Often, however, several directions of variation may be of about equal significance.

As has especially been emphasized by TUOMI-

KOSKI, the systematization of vegetation rests essentially upon the making out of these directions of variation. I think that it may be possible to study them *without* aiming at the construction of a system of the vegetation, and I have recently tried to do this in a synopsis of the vegetation of the North Swedish mires (Bot. notiser 1950).

W. MEIJER: Nach meiner Ansicht soll die Vegetationskunde möglichst weit nachstreben, Probleme zu definieren für weitere ökologische Untersuchungen. Ich glaube, dass die Methode der Schule Zürich-Montpellier dafür nicht immer die am meisten geeignete ist. Besonders zwei Bemerkungen sollen diese Auffassung stützen.

1. Die Treue zwischen Arten ist nicht überall dieselbe. Nach der Methode IVERSENS (Affinitäte ausrechnen) kann man das nachweisen.

2. Mit SCHMID bin ich einig, dass Vegetationen etwas völlig anderes sind als das Gefüge womit man in der Idiosystematik zu tun hat. Man soll um Einheiten zu unterscheiden Diskontinuitäten aufsuchen, und diese liegen in Vegetationen nicht analog zu den Diskontinuitäten, die Anlass geben zu Unterscheidung von Arten in der Idiosystematik.

Man soll die Konsequenz aus dem Eigentümlichen der Vegetationen ziehen und jetzt wagen, ganz neue Wege zu gehen.

Man soll dabei versuchen, mehr anzuknüpfen an die Methoden von IVERSEN, GAMS, TUOMIKOSKI u. a. Sie versuchen, die ökologischen Reihen zu erfassen ohne Scheinbegriffe zu gebrauchen. Wenn man dabei auch nachstrebt, die Vegetationen möglichst weit adäquat, wie ein Mikrobild aufzunehmen, kann man hier mit statistischen Methoden exakter weiterarbeiten und leichter miteinander einig werden.

E. SCHMID: Im tropischen Regenwald kann zunächst nicht auf Grund der Flora gearbeitet werden. Wir müssen mit biologisch-ökologischen Typen, Repräsentationstypen, arbeiten, welche uns erlauben die Struktur zu erfassen. Mit der Repräsentationstypen-Areal-Kurve gibt es hier ein deutliches Bild davon; sie geht in die Horizontale über, die Artenzahl-Areal-Kurve aber nicht!

H. MEUSEL: Das natürliche System der Einzeipflanzen gründet sich auf eine Vielzahl von Merkmalen und deren bestimmte Zuordnung, also bauplanmässige Entsprechungen. Die natürliche Gliederung der Pflanzengesellschaften sollte ebenfalls auf einer Mehrzahl von charakteristischen Merkmalen basiert sein. Die bevorzugte Berücksichtigung von Charakterarten kann nur zu einer künstlichen Gliederung führen. Für eine natürliche Vegetationsgliederung ist vor allem die Verteilung der Gewächse im Erdraum von der zonalen Grossgliederung bis zur Berücksichtigung der Struktur der Pflanzengesellschaften zu berücksichtigen.

C. TROLL: ROTHMALERS Satz „Ökologische Systeme sind nicht realisierbar“ sollte sich wohl nur auf die kleinen spezifischen Pflanzenvereine (Assoziationen usw.) beziehen. Denn neben dem Assoziationsbegriff gibt es auch den klassischen Formationsbegriff. Eine Formation ist aber nicht floristisch, sondern physiognomisch-ökologisch definiert. Die Formationen (z. B. tropischer immergrüner Regenwald, Hochmoor, Mangrovenwald) sind früher erkannt als ihre verschiedenen Assoziationen. Und die Erfassung eines ozeanischen Hochmoors als ökologisch-geographische Einheit darf nicht unmöglich gemacht werden durch seine Aufgliederung in kleinste soziologische Einheiten von hohem Rang (z. B. *Narthecion*- und *Sphagnion*-Verbände).

Welche Ordnung ist natürlich? Die floristische oder die geographisch-ökologische? Ich glaube, das letzte Beispiel muss zeigen, dass die geographische, die *Sphagnum*-Bulten und *Narthecium*-Schlenken zusammenfasst zum *Sphagnum*-Hochmoor, natürlicher ist als die soziologische, die das Hochmoor pulverisiert zu Einheiten, die ganz verschiedenen Verbänden angehören.

N. SÖYRINKI: Ich möchte Prof. MEUSEL nur darauf aufmerksam machen, dass der finnische Pflanzensoziologe und Waldpflanzenforscher Prof. V. KUJALA schon i. J. 1926 in seinen Studien über die finnische Waldvegetation die unterirdische Schichtenfolge der Waldpflanzen-gesellschaften durch ähnliche Profile als diejenigen Prof. MEUSELS geschildert hat.

G. E. DU RIETZ: The divergence between BRAUN-BLANQUET and Scandinavian phytosociologists has been much exaggerated in recent literature. The resolution of the Amsterdam Congress (1935) to stabilize the terms Alliance and Association "in the sense of Zürich-Montpellier plant sociologists", and the term Sociation "in the sense of Scandinavian plant sociologists", was founded upon a proposition presented in complete agreement by BRAUN-BLANQUET, NORDHAGEN and myself. As shown in the works by NORDHAGEN, GJAERREVOLL and myself on Scandinavian alpine vegetation, we are working in Scandinavia with alliances that are easily comparable with those described by BRAUN-BLANQUET from the Alps, and characterized by characteristic and differential species just as those of BRAUN-BLANQUET and his followers. Nor are there any important theoretical divergences in the association concepts used in Scandinavia and in the school of BRAUN-BLANQUET. Contrary to that school, however, we are in Scandinavia still taking a great interest also in the sociations into which most associations are differentiated by means of changing dominants, and we are still concentrating most of our vegetation analysis within these small and homogenous units of vegetation. Also in other respects, our practical methods of vegetation analysis differ largely from those of BRAUN-BLANQUET and his followers, and this leads in some cases to different results in the circumscription of alliances and associations. Since more than 20 years, our Scandinavian phytosociological concepts and working methods are a synthesis of those of BRAUN-BLANQUET and those of the old "Uppsala school".

H. GAMS: Soziationen bzw. Assoziationen sind floristisch zu fassen, aber zunächst zu Konsoziationen mit ökologischen Reihen zusammenzufassen. Aus ökologischen Reihen verschiedener Florengebiete sind die äquivalenten Glieder leicht zu entnehmen und zu Isozönosen (Formationen s. str.) zusammenzufassen.

R. TUOMIKOSKI: We cannot speak of natural classification: it is a *contradictio in adjecto*.

K. HÖFLER: Als Pflanzensoziologe und „neutraler Botaniker“ erkläre ich mich für die floristische Methode. Diese allein gibt m. E. die konstitutiven Merkmale für begriffliche Erfassung der Pflanzengesellschaften. An der so bestimmten Vegetationseinheit hat dann die ökologische Untersuchung einzusetzen.

Der von Prof. E. SCHMID vorgetragenen grundsätzlichen Ablehnung der BRAUN-BLANQUETSchen höheren Vegetationseinheiten muss ich entschieden entgegenreten.

H. OPPENHEIMER also took part in the discussion.

SESSION 9

July 19, 2—5 p. m.

Chairman: H. GAMS, Recorders: G. E. DU RIETZ and H. SJÖRS

SUBJECT:

Vegetation Units (continued), and Various Papers

V. N. SUCATJEV (Moscow)

On the Exploration of the Vegetation of the Soviet Union

The study of the vegetation of the Soviet Union was developed on a particularly large scale after the Great October Revolution in connection with huge works undertaken for the registration of the forage resources (in the tundra, steppes, deserts and alpine regions), with the exploration of forests and the rationalization of forestry, with the exploitation of peat bogs and putting into practice the STALIN plan for the remodelling of nature (in the forest steppes, steppes, deserts) and with other problems of the national economy. Simultaneously works pertaining to theoretical problems regarding studies of plant communities or the phytocoenology (phytosociology) were carried on.

Various maps of the vegetation of the Soviet Union as well as such maps of the various parts of it were drawn up.

The plant community or phytocoenosis served as the initial subject in the study of vegetation, in other words that of any concrete grouping of plants that grow on territories similar according to their characteristics, and is characterized by definite coactions both between plants among themselves and between the plants and their environment. That is why every phyto-

coenosis is characterized by a definite plant composition and by definite environmental conditions.

The basic unit of classification in the studies on plant communities is the plant association which unites all the phytocoenoses that manifest similar coactions between the plants and between the plant and the environment. That is why a plant association is characterized by its definite group of plant species, by a definite structure of its synusies. At the same time each plant association is connected with definite environmental conditions (climate, soil and animals). As it stands here the term plant association has a rather limited meaning bearing similarity to the term "sociation" used by certain authors.

Further development of the ideas of DOKUCHAYEV, BERG, WILLIAMS, MOROSOV, VYSOTSKY and others about the interrelationship of all phenomena and of all objects on the surface of the earth has in the USSR resulted in the conception of the biogeocoenosis (1939, 1945), i. e. a complex of a biocoenosis (phytocoenosis and zoocoenosis) with parts of the atmosphere, lithosphere, hydrosphere and pedosphere which correspond to it. That is why as a rule the limits of a biogeocoenosis are determined by the limits of a plant community. Only the study of the biogeocoenosis as an integral

entity can fully specify the place of the plant communities in nature and their rôle in the rotation of matter and energy.

For the study of the biogeocoenoses in relation to the requirements of the national economy special stations are being set up in the USSR at which, according to specially drawn-up programs, complex explorations by geologists, geomorphologists, hydrologists, climatologists, pedologists, botanists and zoologists are being conducted widely using experiments in nature.

A characteristic feature of Soviet phytocoenology from the very beginning of its development was its historical approach to this problem. Particular attention was always paid to the dynamics of the vegetation and its successions. Recently there has been elaborated a special classification of them differing from that of Western Europe and America.

The application of the dialectical materialism method and of MICHURIN's theory of biology assisted greatly in the profound study of these problems.

Of great importance is the fact that scientists both of the USSR and the West independently came to the conclusion that it was necessary to base the studies of geographical phenomena on the surface of the earth on the related conceptions of the biogeocoenosis, oecotope, etc. Unification of opinion in this field on a correct methodological basis is quite necessary and it shall greatly assist in the development of the study of plant communities since a successful development of phytocoenology and its practical use can progress only in connection with the development of the above-mentioned geographical problems.

Discussion

C. TROLL: Eine gegenseitige Aussprache über die von Herrn SUKACHEV behandelten Forschungswege und Forschungsziele wäre von großem Interesse im Zusammenhang mit der hier geführten Diskussion über „Vegetation Units“. Die russische Forschung strebt wie die der übrigen Länder eine synthetische (physiogra-

phische und biologische) Landschaftsbetrachtung an. Die „Biogeocoenologie“ der russischen Wissenschaft entspricht vollkommen der „Landschaftsökologie“ (vgl. TROLL, Zeitschr. Ges. f. Erdkunde Berlin 1939 u. Studium Generale 1950), die „topoökologischen Einheiten“ der Russen den „Ökotypen“ (TROLL) oder „Sites“ (BOURNE). Das ganze ist ein geographisch-biologisches Konzept, dessen Erfassung durch die Luftbildinterpretation besonders gefördert wurde („Aero-landscape“ nach HAVEMANN u. FAAS 1941). In dieser Richtung wurde in Russland systematischer gearbeitet als in anderen Ländern. Aber die Ähnlichkeit der Ziele und Methoden und die Vielseitigkeit der theoretischen Grundlagen und der praktischen Verwendbarkeit macht eine Aussprache auf internationaler Basis besonders wünschenswert.

V. N. SUKACHEV: The vast scope of scientific activities which is so characteristic of the USSR has also manifested itself in the study of the vegetation in our country. Along with this study, extensive work has been carried on in the development of theoretical views in the field of phytogeography and the associated branches of botany. Since the study of the vegetation was closely connected with the solution of various economic problems on a national scale, this circumstance ensured the methodological correctness of the treatment of theoretical problems. In fact, this is the fundamental feature of the MICHURIN school in biology. Furthermore, owing to the same circumstance, the development of the theory of plant communities was intimately connected with the progress of agronomy, climatology, and other sciences dealing with the study of the environment of vegetation.

In the brief statement which I have made to-day, I have not been in a position to give any detailed description of our achievements, not even in the field of the theory of plant communities. Therefore, I have only touched upon some questions relating to this branch of knowledge, which I consider to be most essential.

Also W. B. TURBILL and H. GAMS took part in the discussion.

R. HEIM (Paris)

Le drame de la protection de la Nature en Afrique

L'addition de causes diverses et concordantes dans leurs effets, nées de la guerre et des circonstances politiques et économiques du monde, particulièrement de l'Europe, a aggravé sérieusement la situation de l'Afrique en ce qui concerne l'état et la protection des ressources naturelles, qui n'ont jamais été aussi compromises.

Difficulté grandissante d'appliquer vis-à-vis du braconnage les mesures répressives auprès des indigènes en raison de leur nouveau statut politique, diffusion des armes à feu parmi eux, délits de chasse dont les Européens, y compris les plus hauts fonctionnaires, se montrent coupables, développement des troupeaux domestiques, emploi de l'anthrycide, mesures destructives prises en Afrique du Sud contre le gros gibier, augmentation de la population noire et de ses besoins, méconnaissance par les Blancs des lois fondamentales de la protection des sols et de la vie sauvage sous les tropiques.

Intensification de la monoculture industrielle aux dépens des terres et des cultures vivrières, efforts insuffisamment préparés des planned enterprises (aménagement du Niger, ground nut scheme, développement de la culture du riz sur pentes, exploitation mécanisée de la forêt tropicale au Camérout, au Gabon, en Côte-d'Ivoire).

Ainsi, les louables efforts menés par les organismes nationaux et internationaux (Unesco, Union Internationale pour la Protection de la Nature, etc.) se heurtent aux plans des économistes et des hommes d'affaires, trop souvent conseillers des gouvernements, dont les fonctionnaires ignorent fréquemment les lois essentielles de l'évolution, de la protection et de la mise en valeur de la forêt et des sols tropicaux et le fait essentiel que l'Afrique dans son ensemble reste une terre pauvre, inapte à supporter des méthodes de culture européennes.

Impuissance de la Loi. Inefficacité ou leurre du contrôle. Seuls permettront la sauvegarde des dernières ressources renouvelables en Afrique: 1°) Une charte internationale pour la pro-

tection de la Nature. 2°) L'éducation des masses à la fois européennes et indigènes, de l'élite, des gouvernements, par un pressant mouvement né d'une pression exercée par les grands organismes internationaux, et par un programme éducatif, précis, souple, qui utiliserait la radio, l'image, la brochure, l'enseignement scolaire et universitaire, la presse. 3°) La création d'un Bureau Interafricain d'informations sur la conservation et l'utilisation des sols. 4°) L'adoption autant qu'il est possible d'une formule mixte d'exploitation élevage-jachères.

Nécessité de renouveler le cri d'alarme.

Discussion

G. POTTIER-ALAPETITE: En Afrique du Nord le problème se pose également. Les ennemis de la végétation sont les troupeaux (chèvres) et l'homme. Dans toute la région centrale de la Tunisie, p. e., il n'y a pas de végétation arborescente. — Les paysans et les nomades, pour faire le feu domestique vont arracher les racines des plantes vivaces qui sont leur seul combustible. Du fait de l'augmentation de la population, qui est dans de meilleures conditions hygiéniques, cette dévastation s'accélère peu à peu — et l'érosion s'aggrave.

Il ne suffira pas de défendre, il faudrait aussi fournir aux populations le moyen de vivre. — Un organisme international semble seul qualifié pour trouver et imposer des solutions rationnelles.

W. ROBYNS: 1. Dans la protection de la nature il s'agit en premier lieu de protéger la végétation, ce qui conservera et la faune et le sol.

2. Il faut tenir compte aussi de l'action des facteurs naturelles, qui se modifient lentement et provoquent des modifications lentes de la végétation, de la faune et du sol.

H. HUMBERT also took part in the discussion.

M. SCHWICKERATH (Aachen)

Das Ganzheitsprinzip in seiner Bedeutung für die Formung des Assoziationsprinzips

Im Anschluss an JACOB VON ÜXKÜLL werden kurz die verschiedenen Weltanschauungswellen, die über die Menschheit des abendländischen

Kulturkreises in den letzten 500 Jahren dahingegangen sind, gekennzeichnet. Es wird auf die enge Verknüpfung des Ganzheitsprinzips mit der neu aufsteigenden biologischen Weltanschauungswelle hingewiesen. Das Lebensprinzip für das Einzelwesen wird erläutert und als seine wichtigsten Bestandteile werden das Ausgleichs- und Richtungsprinzip, die allgemeinste Bedeutung haben, aufgezeigt. Dann erst wird das Ganzheitsprinzip dargelegt und die eigengesetzlichen Ganzheiten von den fremdgesetzlichen geschieden. Aus der Darlegung springt heraus: Ausgleich- und Richtungsprinzip sind auch die wesentlichsten Bestandteile des Ganzheitsprinzips.

Die Ganzheit des Einzelwesens wird in Beziehung gesetzt zur Lebensgemeinschaft. Auch die Lebensgemeinschaft, hier in ihrem pflanzlichen Aufbau d. h. in der Pflanzengesellschaft erfasst, ist eine Ganzheit oder wenigstens ganzheitlicher Betrachtung zugänglich. Zwar darf sie nicht mit der Lebensganzheit des Organismus gleichgesetzt werden. So ergibt sich die Scheidung von Lebensganzheit des Einzelwesens und lebendiger Ganzheit oder organischer Ganzheit der Gemeinschaft von Einzelwesen. Ihre Verwandtschaft ist nicht nur bildhaft sondern wesentlich.

Aus diesen Gedankengängen wird für den einen grundlegenden Begriff der Pflanzensoziologie, für den Assoziationsbegriff, folgende Forderung gezogen: „Der Assoziationsbegriff soll schon in seiner Formung möglichst klar das Ausgleich- und Richtungsprinzip erkennen lassen.“ Diese Forderung kann erfüllt werden, wenn man der Charakterartenmethode durch eine umfassende Anwendung des Richtungsprinzips das letzte Statische nimmt und die Assoziation somit zu einem völlig dynamischen Begriff gestaltet.

Für das Beispiel des *Violetum calaminariae* wird an einem Modell in der Verknüpfung der Charakterarten und der hoch-steten Begleiter das Ausgleichprinzip und in den polar gegenüberstehenden Differentialarten der kalkreichen und kalkarmen Varianten das Richtungsprinzip veranschaulicht.

Zuletzt wird auf die aus dem Richtungsprinzip erspriessende Möglichkeit der geographischen Differentialarten hingewiesen. Ihre Bedeutung und Zweckmässigkeit wird am *Xerobrometum erecti* entwickelt. Das Abbild, das der neuartig gegliederten Gesamtassoziation zugeordnet wird, weist jeder Art des *Xerobrometum erecti* qualitativ und quantitativ seine soziologische und florengeographische Stellung an und lässt mit einem Blick Aufbau und Verbreitung der Gesellschaft erfassen.

Damit wird aber auch Pflanzensoziologie und Pflanzengeographie wieder enger verknüpft. Auch die Transformation der Konstantenmethode in die Charakterartenmethode gelingt mit dem umfassend genutzten Differentialartenbegriff.

J. J. BARKMAN (Leiden) *Some Proposals for a Phytosociological Nomenclature*

Because of the still lacking uniformity in phytosociological nomenclature internationally accepted rules are highly desirable. This paper gives some suggestions in that direction.

We should follow as closely as possible the ideas of the idiotaxonomical nomenclature. Only those associations are proposed to be considered as valid which are accompanied in the publication by a table of at least 10 releves (sub-associations 5, facies 1 relevee). Introduction of type releves is proposed: each author should indicate which of his simultaneously published releves is considered by him as the type relevee. Of units already described the author or else a specialist should elect a type relevee (lectotype). Indication of the exact locality of the type vegetation is necessary.

The principle of priority should be applied in phytosociological nomenclature. Legitimate is the first validly published name of an unit. Vegetation units should always be cited with the name of their author; the articles 46-49 of the international rules of botanical nomenclature should be followed here (*mutatis mutandis*).

As to the validity of units of higher rank it

should be considered sufficient if the author indicates which units of lower rank belong to this unit. As type association of an alliance the first validly described association of this alliance has to be considered. If an association or an alliance has to be split up, the original name should be reserved for the association (or alliance), to which the original type relevee (or type association) belongs.

Names of units should be formed more or less in the way indicated by BRAUN-BLANQUET from the root of the Latin generic name of a species, which is characteristic of, or at least occurs in, the unit concerned. Geographical epithets are allowed, but should be avoided if possible. Contracted names, established with the purpose to avoid too long names (e. g. the *Polamion*) should be considered individually in order to see whether they can be maintained as *nomina conservanda*. Names of vegetational units should be independent from changes in the nomenclature of the species from which they are derived. If a species is considered to belong to different genera by different authors, the author of the vegetation unit is completely free to choose after which of these names he wants to name his vegetation unit. If, however, a group of species are either considered all to belong to a genus A or all to a genus B, and several associations are named after species of such a group, all associations should be derived from the same generic name.

If a vegetation unit has been validly described and its name has not been formed according to the rules given above, this unit cannot therefore be neglected and redescribed by another author; its name must be brought in conformity with these rules, but it should keep the author's name of the person who published the table of relevees.

At last uniform Latin terms are proposed for the various ranks of vegetational units, based upon those proposed by DU RUIZ (1930), particularly the term *federation* for alliance and the terms *socium*, *associon* and *federion* for *synusia* of different *synsystematical* rank, terms to which the term *subassocion* could be added.

Literature

- G. E. DU RUIZ, 1930: Vegetationsforschung auf soziationsanalytischer Grundlage. ABERHALDEN'S Handbuch der biologischen Arbeitsmethoden, Abt. 11, T. 5, S. 273—480.

Discussion

J. BRAUN-BLANQUET: Begrüsst die Vorschläge von BARKMAN und möchte sie zur Diskussion der zu gründenden Kommission zuweisen.

Ist einverstanden mit einer möglichst breiten Basis, die natürlich auch Osteuropa umfassen soll. Vorschläge wären erwünscht. Gerade eine Kommission wird aber zu engerer Zusammenarbeit Veranlassung geben können.

Die Kommission soll nicht apodiktische Beschlüsse fassen. Sie soll Eingaben, Vorschläge prüfen und nach eingehendem Studium dem nächsten Kongress unterbreiten.

Gerade das immer engere Zusammenarbeiten mit den Praktikern nötigt dazu, Auswüchse bei der Aufstellung und Benennung der Pflanzengesellschaften zu bekämpfen.

Zusammenarbeit mit den Pflanzengeographen erwünscht, aber die Pflanzengeographen sollen den Pflanzensoziologen, die im Feld praktisch arbeiten, nicht in ihre Arbeitsmethoden reden.

H. MEUSEL: Eine zu starke Betonung von Nomenklaturfragen könnte leicht zu unerfreulichen Diskussionen führen, die das Ansehen unserer Arbeitsrichtung nur schädigen. Gegen die Aufstellung von Nomenklaturregeln entsprechend denen der Taxonomie spricht aber vor allem die Tatsache, dass es gar nicht möglich ist, streng festgelegte Vegetationseinheiten abzugrenzen. Der Vegetation fehlen die geschlossenen organismischen Einheiten. Die Vegetationsbetrachtung muss deshalb ebenso wert legen auf Übergänge und Vermischungen von Gesellschaften, wie auf die Abgrenzung bestimmter Typen. Den Einheiten kommt nicht der Wert zu, wie in der Taxonomie.

Eine notwendige allgemeine Verständigung im Hinblick auf die Vegetationsgliederung kann erst erreicht werden auf Grund einer umfassenden Kenntnis grosser Gebiete. Dabei ist vor

allen die räumliche Gliederung der Vegetation zu beachten. Eine Trennung in Pflanzengeographie und Pflanzensoziologie führt zu unnatürlichen Einteilungsprinzipien. Deshalb folgende Vorschläge:

1. Die Kommission zu erweitern durch Einbeziehung von Pflanzensoziologen und Pflanzengeographen aller Arbeitsrichtungen.

2. Zusammenarbeit auf breiter Basis, die die Voraussetzung schafft für die Vegetationsgliederung von ganz Europa. Dabei Berücksichtigung der Vegetation Osteuropas und ihrer Erforschung.

3. Zurückstellen von Nomenklaturregeln bis eine einheitliche Auffassung über Vegetationsgliederung erreicht ist, die, nach der Entwicklung der verschiedenen Schulen zu urteilen, in absehbarer Zeit möglich sein wird.

G. E. DU RUIZ: The introduction of any law of priority into phytosociological nomenclature would be the most destructive thing that could happen to phytosociology. The first name given to an alliance or to an association is usually very tentative and often very bad, sometimes giving a very wrong idea about the true indicator species of the biocoenose concerned, because it was given at a time when very little was known about the natural differentiation of the biocoenoses and about their characteristic and differential species. The conservation of such names by any law of priority would lead to permanent errors and confusion, and would thus hamper the progress of phytosociological science instead of promoting it. Obviously it can be of no use whatever to conserve an alliance or association name based upon a species once supposed to belong to the characteristic or differential species of the biocoenose concerned but shown by more profound researches not to belong to these species, and to reject a later name of the same biocoenose based upon a species which really belongs to the most important characteristic species of the biocoenose concerned. The names used for a plant community should be based upon real monographic work, not upon the first superficial study of the community. Let the various names proposed

for a plant community enter into free competition among phytosociologists, and let the name based upon the soundest and most reliable arguments become the final name of the community.

As to BARKMAN's proposition of conserving some of the terms proposed by myself in 1930, it must be kept in mind that the terms *socion*, *consocion*, *associon* and *federion* were abandoned already in 1935 by agreement between GAMS, LIPPMAA and myself, i. e. the three phytosociologists of that time working most with *synusia*, and replaced by the terms *society*, *union* and *federation* for the three lowest units in the hierarchy of *synusia*. The term *federation* can, therefore, not be taken up again as an international term for the unit now very aptly called *alliance* in English and French, and *Verband* in German.

K. FÆGRI: Because of the fundamental difference between taxonomy and phytosociology with regard to agreement as to the methods of descriptions of units, the apparent parallelism between taxonomic and phytosociologic nomenclature is a false analogy.

The speaker proposed the following two recommendations to be accepted by the section and forwarded to the plenary session of the Congress.

Recommendation 1

The section PHG of the 7th International Congress considers that phytosociologists should in the future include in the description of phytosociologic units of whatever order a representative list of the species forming the community, if possible with indications of quantitative relations based upon statistical investigations.

K. FÆGRI

Recommendation 2

Because the fundamental concepts in phytosociology are still matters of dispute, and because the techniques of description of phytosociologic units are — as a consequence of the above-mentioned disagreement — still widely varying, the section PHG of the 7th International Botanical Congress considers it premature

to lay down at the present moment more definite rules as to the nomenclature of phytosociologic units than those terminologic principles which were agreed upon by the 6th International Botanical Congress.

K. FAEGRI

M. GUINOCHE: Bien que jugeant le cadre proposé par M. BARKMAN comme trop rigide, il a néanmoins le grand avantage de provoquer une discussion sur le sujet important. Je pense, comme M. le Prof. DU RIETZ, qu'une règle de priorité trop absolue pourrait être gênante; mais, d'accord avec M. le Prof. FAEGRI, j'estime qu'un tableau de relevés est nécessaire pour définir un groupement. Quoiqu'il en soit, il n'est pas possible de discuter tous les points dans une réunion comme celle-ci. Ceci est également l'avis d'un certain nombre de nos collègues qui m'ont chargé de présenter en leur nom un vœu pour la création d'une commission chargée de préparer des propositions pour le prochain congrès et dont je vais me permettre de vous donner lecture. J'ajouterai que cette commission n'aurait pas pour mission de remettre en question les points de doctrine sur lesquels on s'était mis d'accord à Amsterdam, mais uniquement de proposer quelques règles simples, sauvegardant à la fois la liberté et la propriété scientifique ainsi que le bon sens.

W. MEIJER: Die Vorlesung des Herrn BARKMAN ist ganz geeignet, dem prinzipiellsten Punkt der Vegetationsforschung Schaden zu tun. Seine Auffassung „we should follow as closely as possible the ideas of the idiotaxonomical nomenclature“ ist eine Konsequenz der Methode, die nach Analogie der Idiosystematik Assoziationen, Ordnungen und Klassen aufgestellt hat. Man soll aber der Sache zuerst eine bessere philosophische Grundlage geben, und vielleicht können wir dann darüber einig werden, dass das Gefüge von Vegetationen so weit von dem Gefüge des Organismenreiches verschieden ist, dass wir ganz andere Methoden und Einteilungen brauchen.

Das sollte zuerst weiter diskutiert werden, bevor man über Nomenklatur spricht.

J. J. BARKMAN: An Herrn H. MEUSEL: Auch

jetzt schon werden Vegetationseinheiten vielfach zusammen mit ihren Autorsnamen zitiert. Die Gefahr, dass unzählige Einheiten auf ungenügenden Gründen aufgestellt werden würden, nur weil der Autor seinen Namen an eine Einheit verbinden will, besteht also auch jetzt schon und wird gerade von der Prioritätsregel eingeschränkt werden.

To Prof. DU RIETZ: To your objection that many names of associations given by an author turn out to be non-characteristic when his experience increases and that according to the priority rule still the former names should have to be conserved, one could answer that we could find a compromise, taking as a starting point for nomenclature a rather late date, as e.g. 1930. Moreover it seems not so important whether a name is characteristic or not, if only everybody knows what is meant by it.

Of course every method and school should be respected; in order to do that, one could restrict the rules — at least the details of them — which I gave in my paper, to the Zürich-Montpellier school, or establish (partly) different rules for the other schools.

To Prof. FAEGRI: We cannot help that representatives of other than the Uppsala and the Zürich-Montpellier schools are not present at this moment. However, in the proposal for an international phytosociological commission also members of other schools are invited to take part.

I cannot believe that the rules given in this paper would not be obeyed, in case they were accepted by a representative international commission.

An Herrn W. MEIJER: Die Frage der Erforderlichkeit einer philosophischen Grundlage ist schon heute morgen erörtert worden und kann also hier übergangen werden. Ich möchte nur erwähnen, dass gerade das Aufzwingen einer bestimmten philosophischen Grundlage für die Phytosoziologen wohl eine Einschränkung der wissenschaftlichen Freiheit darstellen würde.

E. DAHL: I quite agree with the contents of the first proposal of professor FAEGRI but I object to this use of the word statistical meth-

ods. Most tables of vegetation analyses are not statistical tables as the word statistics is employed in other branches of science. The so-called "statistical" method of analysis of vegetation is only a standardized method of description which permits a qualitative comparison of the analyses.

W. ROTHMALER also took part in the discussion.

Prof. FAEGRI's two proposals were accepted by the Section and later by the Third Plenary Session.

Prof. FAEGRI suggested a new wording of prof. GUINOCHET's proposal.

W. LÜDI: Im Antrag GUINOCHETS ist die Rede von einer commission d'écologie géographique, die in Cambridge gewählt worden sei und der die pflanzensoziologische Kommission als Subkommission angegliedert werden soll. Ich frage an, was für eine Kommission das ist, wer ihr angehört und was sie bisher geleistet hat.

An informal discussion followed. The voting was postponed. The proposal by GUINOCHET and FAEGRI about an international commission working on problems of phytosociology was read again by FAEGRI after REGEL's paper. It was accepted next day as the following recommendation, but not passed by the Congress Plenary Session, because of lack of time:

La section de phytogéographie du VIII^e congrès international de botanique, jugeant nécessaire une entente de la coordination des travaux phytosociologiques émet le vœu que

1. soit immédiatement constituée une commission chargée de préparer des propositions pour le VIII^e congrès international de botanique.

2. que cette commission soit rattachée d'une manière efficace à l'Union Internationale des sciences biologiques.

Members of the committee:

BHARUCHA	DANSEREAU
BOLOS	DAUBENMIRE
BOYKO	DU RIETZ
BRAUN-BLANQUET	FAEGRI
CAIN	GAMS

GIACOMINI	OBERDORFER
GODWIN	PINTO DA SILVA
GUINOCHET	ROTHMALER
HÖFLER	SCHMID
HORVAT	TADRAS
IVERSEN	TROLL
KLIKA	TUOMIKOSKI
W. KOCH	TÜXEN
LEBRUN	v. SOÓ
LÜDI	WEBB
MANGENOT	WESTHOFF
MEUSEL	
MOLINIER	The Academy of
NORDHAGEN	Sciences of the USSR
PARODI	should be approached.
PAWLOWSKI	

The commission may supplement itself with not more than 5 members from countries which are at present under-represented.

Rapporteur: GUINOCHET
Secrétaire: FAEGRI.

It was later decided to refer PINTO DA SILVA's proposal for an Index des groupements végétaux to the committee for appropriate action.

A. R. PINTO DA SILVA (Sacavem) *L'index des groupements végétaux.* *Proposition pour sa réalisation*

La Géobotanique intéresse de plus en plus et de jour en jour les chercheurs d'autres régions. La bibliographie concernant l'étude des groupements végétaux s'élargit rapidement et se répand parmi de nombreuses publications.

Les systématiciens ont reconnu qu'il était nécessaire d'établir des règles de nomenclature et ils ont reconnu aussi l'utilité de certaines oeuvres auxiliaires qui facilitent et règlent leur travail, en essayant d'en réaliser d'autres dont l'absence se fait sentir encore. Il me semble utile de profiter de l'expérience de la Systématique et du fait que la Géobotanique est encore récente. Toute solution deviendra plus complexe, plus lourde, voire même impossible, si l'on retarde l'organisation du travail scientifique dans ce domaine.

Sous les criteriums, les plus divers (que nous ne nous proposons pas de discuter ici) on établit pour désigner les groupements végétaux, des noms, pas toujours expressifs, qui ne peuvent jouer que très partiellement un rôle descriptif.

En formulant cette proposition, dont l'essence est sans doute dans la pensée de tous, je ne voulais que profiter de l'occasion donnée par ce Congrès et essayer de résoudre ce problème en créant un instrument de travail utile à tous ceux qui s'intéressent aux études de la végétation. Je n'oserais pas présenter en détail les caractéristiques d'un tel *Index des Groupements Végétaux* et je ne veux pas, plus, abuser du temps dont on dispose ici. Je me borne, par conséquent, à suggérer quelques bases (que je considère nécessaires pour l'éclaircissement de cette idée) et je propose au Congrès la création d'une Commission pour élaborer un projet qui serait réalisé par l'organisme que l'on considère approprié, si ma proposition est approuvée. Voici ces bases:

I — L'INDEX DES GROUPEMENTS VÉGÉTAUX contiendra tous les noms créés pour désigner les groupements, ainsi que les unités supérieures et les subdivisions distinguées, quelle que soit la nomenclature qu'ils présentent et à partir d'une date à fixer.

II — La synonymie sera donnée seulement quand elle est indiquée dans l'original d'où le nom a été tiré.

III — On doit indiquer en abrégé et par des signes conventionnels: la catégorie donnée au groupement ou unité; la référence bibliographique et la date de publication; la distribution géographique du groupement; la documentation sur laquelle le groupement s'appuie, telle que: tableaux, diagnoses, noms de caractéristiques, relevés, listes, etc. ou absence de documentation (noms nus).

Discussion

CH. SAUVAGE: La commission dont M. PINTO DA SILVA préconise la création pourrait être la même que celle proposée par M. GUINOCHET; il serait bon que la section PHG se prononce

par un vote sur l'ensemble de ces deux propositions.

M. GUINOCHET also took part in the discussion.

C. RECEL (Zürich)

La limite entre l'Europe Centrale et la région de la Méditerranée

La limite entre l'Europe Centrale et la région de la Méditerranée dépend des lois suivantes:

La loi «Nord-Sud» influence l'alternation des grandes zones climatiques et de paysage, du nord vers le sud, la zone arctique, boréale, némorale, des steppes et du désert.

La loi «Est-Ouest (Centre-périphérie)» influence l'étendue de l'influence océanique (en Europe l'influence atlantique) et continentale dans chacune de ces zones. La région de la Méditerranée n'est que la partie atlantique de la zone des steppes.

La loi promulguée par le soussigné: «la limite supérieure des forêts dans une montagne est constituée par le climat de la zone située au nord de cette montagne». Dans les montagnes de la zone boréale elle est constituée par les forêts à bouleau du nord, dans les montagnes de la zone némorale par les forêts à épicéa de la zone boréale, dans les montagnes de la zone des steppes (y compris celles de la Méditerranée) par les forêts à feuilles caduques de la zone némorale, dans les montagnes de la zone des déserts par les forêts à feuilles persistantes de la région de la Méditerranée ou par la steppe.

La limite entre l'Europe Centrale, faisant partie de la zone némorale, se trouve là, où dans la plaine commencent à paraître les forêts à feuilles persistantes et où la limite supérieure des forêts est constituée non par des forêts à épicéa, mais par des forêts à feuilles caduques, comme p. e. par le *Fagus sylvatica* en Italie et dans la presqu'île du Balkan. La limite méridionale de la partie septentrionale de la région méditerranéenne se trouve là, où la limite supérieure des forêts est constituée non par le *Fagus sylvatica*, mais par des conifères de la Méditerranée, comme p. e. *Abies cepha-*

lonica, *Abies Bornmülleriana*, *Cupressus sempervirens*, *Pinus Heldreichii*, *Cedrus atlantica* etc. L'intérieur des grandes presqu'îles de la région de la Méditerranée, celles des Pyrénées, des Apennins, des Balkans, de l'Asie Mineure, est couverte d'une végétation de Steppe dans la plaine ou bien d'une végétation oréophile dans les montagnes. Le caractère de la végétation oréophile et la répartition des étages varie dans les régions différentes. Il faut distinguer la montagne de l'Europe Centrale de celle de la région de la Méditerranée septentrionale et de la Méditerranée méridionale. L'Apennin et les montagnes de la Grèce septentrionale et centrale appartiennent au type des montagnes de la Méditerranée septentrionale, celles du Péloponèse et de la Crète au type de la Méditerranée méridionale, les montagnes de la presqu'île des

Balkans septentrionale et les Alpes Maritimes au nord de Nice (p. e. Vésubio) et les Pyrénées sont du type des montagnes de l'Europe centrale. Sur la presqu'île des Balkans la limite entre l'Europe Centrale passe le long des Rhodopes pour monter vers le nord le long de la côte de la Mer Adriatique. La partie méridionale de la zone némorale est constituée dans sa partie occidentale par des forêts à *Quercus pubescens*, qui touchent les forêts à feuilles persistantes de la région de la Méditerranée. A l'est la partie méridionale de la zone némorale est constituée par la steppe boisée (Lesostep des russes, Waldsteppe), qui confine à la steppe. L'intérieur de la presqu'île des Balkans (Macédoine yougoslave et Bulgarie) et les Alpes Maritimes sauf une étroite bande le long de la côte font part de l'Europe Centrale.

SESSION 10

July 20th, 9 a. m. — 1 p. m.

Chairman: F. R. BHARUCHA, Records: G. E. DU RIETZ and H. SJÖRS

SUBJECT:

Climatic and Secondary Grassland Vegetation

MOHAMMED DRAR (Cairo)

The Problem of the Sudd in Relation to Stabilizing and Smothering Plants

The term "Sudd" is generally applied to the depression of the White Nile, which is covered with dense swamp vegetation. About 50% of the Nile discharge is lost by evaporation and transpiration in this area. The most abundant species here are *Cyperus Papyrus* L. v. *antiquorum* C. B. Cl. and *Vossia cuspidata* Griff. These grow either separately or frequently intermixed with other species mainly belonging to the genera *Phragmites*, *Typha*, *Echinochloa*, *Luffa*, *Ipomoea*, *Cissus*, *Vigna*, etc.

A distance of about 150 km, north of the depression, is permanently under water because the river has no banks. In the middle part, twice as much as this distance is only flooded

during the high level period of the river, whereas a similar distance on the southern side is never flooded owing to higher banks. It is mainly through the first two parts that the water escapes to the depression turning it to one great swamp.

The need of Egypt for more water in the near future is quite obvious and the principal projects to reduce this loss are (a) to embank the river course, or (b) to cut an auxiliary canal outside the swamp. The first project is considered cheapest and the other as the most expensive.

The writer had the chance of sailing through this depression and believes that if the system of raising banks by suitable trees and shrubs is followed, considerable water loss could be prevented and the expense of embanking would be greatly reduced. The use of plants to raise level by silting is not an uncommon practice through-

out the world and the writer has, a few years ago, introduced this system to the King's Island at Aswan; the application of which finally yielded more land to the area of this little island.

Suitable elements for the greater part of the Sudd are not lacking among the natural vegetation of the Sudan and the following are some of the species noticed by the writer in the seasonally inundated areas: *Acacia campylacantha* Hochst., *A. Sieberiana* DC., *A. arabica* Willd., *Celtis integrifolia* Lam., *Oxytenanthera abyssinica* Munro, *Salix Murielii* Skan., *Ficus capraefolia* Del.

Owing to the difficulty of propagating vegetatively such trees as those of the first four species, much more suitable elements could be selected from among cultivated plants, e.g.: *Salix babylonica* L., *S. Sajsaf* Forssk., *S. tetrasperma* Roxb., *Populus euphratica* Oliv., *Morus indica* L., *Tamarix articulata* Vahl, *Bambusa arundinaria* Retz., *Dendrocalamus strictus* Nees, etc. In the selection of trees priority should be given to those species which have (a) wide range in water tolerance, (b) vigorous root system, (c) freely suckering habit, (d) comparatively quick growth, and (e) easy multiplication directly on the spot. The shrubs should also be of species that could flourish better under weak illumination than in direct sunlight, e.g.: *Lantana Camara* L., *Duranta Plumieri* Jacq., *Tithonia diversifolia* Gray, *Clerodendron fragrans* Vent. *C. siphonanthus* R. Br., *Cupea Llavea* Lindl. *Canna indica* L., etc.

As the water control schemes will not be fully developed before another twenty years, there would be ample time for detailed study and improvement of our present knowledge on the possibilities of tree planting. The experiments proposed should firstly be applied along the line of banks which are inundated at present, periodically, before tackling the permanently flooded area, which is apparently more difficult. The planting of lines of trees together with a background of shrubs would stabilize the present low banks, hold up humus and silt brought down by the annual torrents and finally help to

raise the level of these banks. This scheme should be immediately applied to the southernmost high banks, which are never flooded now, to fix the soil and stop unavoidable erosion due to annual torrents.

The construction of the auxiliary canal would necessarily lower the level of the river itself and thus the drained space would soon become infested with swamp vegetation unless checking elements are employed. Even in this case, the banking of the original river is foreseen and the need of stabilizing and smothering plants is quite apparent.

Discussion

A. S. THOMAS: The problem of reclaiming papyrus swamps has been much studied in Uganda, where species of *Eucalyptus* have been found the best trees to plant; reference a paper by EGELING. It seems to me that it might be difficult to stabilize the papyrus and dry it out, as much of it might be floating on water, and that some of the species, e.g. *Oxytenanthera abyssinica*, mentioned by DRAR might have been growing on termite mounds, for in Uganda they did not tolerate wet conditions.

M. DRAR: I wish to thank Mr. THOMAS of whom I heard a lot during the Congress about his work in Uganda on the problem of draining marshes, but whom I have the chance to meet only at this moment. — Certainly *Acacia Seyal* is one of the best species for this purpose. It is in fact in my list of recommendations. But I wish to draw attention to a species which stands wet conditions much more satisfactorily. This is *Acacia Verek* which is found in the immediate banks throughout the southern part of the Sudan. Regarding the possibility of trees growing in the permanent swamp I wish to emphasize that there are trees which I have actually seen under this condition, and I projected some of them in the lantern. Regarding termites and trees, we have to find out which of them begin first. — The problem is to commence from now on preserving the high banks, stabilizing and raising the level of the annually inundated parts.

Thus we would learn more of how to carry on our work to the more difficult part, that is the permanent swamp.

C. TROLL (Bonn)

Savannentypen und das Problem der Primärsavannen

Der Begriff der Savannen — seit A. GRISEBACH als die Grundform des Pflanzenwuchses in den wechselfeuchten Tropen betrachtet — wird heute ganz verschieden aufgefasst, entweder rein physiognomisch nach dem Anteil von Gräsern und Holzgewächsen (O. DRUDE und A. F. W. SCHIMPER) unabhängig von dem Grad der Trockenheit, oder aber ökologisch nach dem Grad der klimatischen Feuchtigkeit. Im ersten Falle hat man „Savannen“ (von Baum- und Waldinseln durchsetzte Grasfluren) und reine „Grassteppen“ unterschieden, im zweiten Fall dagegen hat man — vornehmlich von geographischer Seite — den tropischen Graslandgürtel gegliedert in einen feuchteren Savannen-(Hochgras-)Gürtel und einen trockeneren Steppen-(Kurzgras-)Gürtel. Andere Geographen vermeiden das Wort Savanne ganz und sprechen nur von tropischen Feuchtsteppen und Trockensteppen, während sich neuerdings mehr und mehr der Vorschlag durchsetzt, das Wort Steppe für die Tropen ganz zu vermeiden und von tropischen Savannen verschiedenen Feuchtigkeitsgrades (Feuchtsavanne–Trockensavanne–Dornsavanne) zu sprechen. Dabei versteht man unter Savanne einen klimatischen Vegetationsgürtel und muss, da der Anteil von Graswuchs und Holzwuchs von lokalen, edaphischen, biotischen und anthropogenen Faktoren bestimmt wird, physiognomisch noch jeweils zwischen Grassavannen und Savannenwäldern unterscheiden.

Im Folgenden ist von Grasfluren des Feuchtsavannengürtels und des Trockensavannengürtels die Rede. Es wird zu zeigen versucht, welche edaphischen und biotischen Faktoren für das Auftreten und die Verteilung von hygrophilen, immergrünen Waldinseln innerhalb der

Savannen massgebend sind. Diese aus Arten des Regenwaldes gebildeten Waldinseln und Waldstreifen, die an Stellen günstiger Wasser- und Bodenverhältnisse entstehen, nämlich dort wo auch in der trockenen Jahreszeit ein günstiger Wasserhaushalt gesichert ist, sind ökologisch scharf zu trennen von den dem Wassermangel der Trockenzeit ausgesetzten und der Trockenruhe unterworfenen sonstigen Bäumen und Gehölzen der Savanne. Auch bei ihrer Verteilung spielen edaphische Verhältnisse eine grosse Rolle, daneben aber auch anthropogene Einflüsse. Im allgemeinen macht man die Erfahrung, dass auf steinigem, gut durchlüftetem Substrat bei tiefem Grundwasserstand das Auftreten der Gehölze begünstigt wird, während auf ebenem, alluvialem, namentlich feinkörnigem, schwerem Boden bei geringer Grundwassertiefe der Baumwuchs behindert und die reine Grasflur bevorzugt wird. Aber auch der Grasbrand, der in die hygrophilen Waldinseln nicht einzudringen vermag, da ihnen der Grasunterwuchs fehlt, spielt mit seiner ungeheuren selektiven Wirkung für die Zusammensetzung und das Aussehen der tropischen Grasländer bekanntlich eine sehr grosse Rolle.

Nach dem Vorkommen und der Verteilung der hygrophilen Waldinseln seien folgende Typen unterschieden (vgl. Abb. 1):

1. Galeriewald-Savannen

Allgemein bekannt ist das Auftreten hygrophiler Uferwaldstreifen in den Savannenebenen, wie sie PIAGGIA aus dem oberen Nilgebiet als „Galerien“ beschrieben hat. Sie treten dort auf, wo in eine trockene Grasebene Fluss- und Bachtäler eingeschnitten sind, in deren Talaue durch das Grundwasser die ganzjährige Wasserversorgung gesichert ist (Riverine Forest, Fringing Forest). Die trockene Ebene, die von einem Netzwerk immergrüner Galeriewälder durchzogen ist, trägt selbst Grassavanne, ist baumfrei oder mehr oder weniger von brandharten, laubwerfenden oder hartblättrigen Bäumen und Büschen durchsetzt. Die Hänge der Berge haben meist dichteren Baumwuchs trophiler Hölzer.

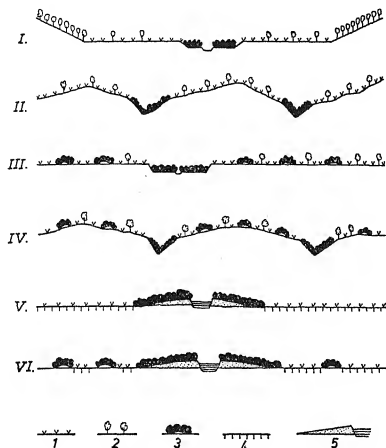


Abb. 1. Savantentypen, nach dem Anteil und der Anordnung von hygrophilen Gehölzinseln.

- I. Galeriewald-Savanne (Savane à Forêt-Galerie)
- II. Schluchtwald-Savanne (Savane à Forêt de Ravines)
- III. Galeriewald-Termitenwald-Savanne (Savane à Forêt Galerie et de Termitières)
- IV. Schluchtwald-Termitenwald-Savanne (Savane à Forêt de Ravines et de Termitières)
- V. Dammuferwald-Savanne oder Bancowald-Savanne (Savane à Forêt de Bancos)
- VI. Banco-Isa-Savanne (Dammuferwald-Termiten-Savanne) (Savane à Forêt de Bancos et de Termitières)

1. Grasflur 2. Tropophile Hölzer 3. Hygrophile Gehölze
4. Tonboden der Überschwemmungssavannen 5. Aufschüttungen der Bancos.

2. Schluchtwald-Savannen

In bergigen und hügeligen Savannenlandschaften weitverbreitet ist ein anderer Typ, den ich Schluchtwald-Savanne genannt habe. Dabei sind die hygrophilen Waldstreifen auf die steil eingeschnittenen, engen Schluchten beschränkt, wo sie vom Bachbett bis zum oberen Rand der Schlucht reichen und sich häufig in den Quellmulden noch besonders verbreitern. Das freie Gelände zwischen den Tälchen, die sanfter geböschten Riedelflächen, sind von offenen Grasfluren überzogen und von einzelnen tropophilen

Bäumen und Büschen durchsetzt. Sie unterliegen dem Grasbrand, der am Rande der Schluchtwälder sein Ende erreicht. Der hygrophile Wald der Schluchten ist zum Teil bodenkundlich durch die frischen A/C-Böden (im Gegensatz zu den schweren Laterit-, Rotlehm- und Eisenkrustenböden der offenen Flächen), z. T. durch das Bodenwasser, z. T. mikroklimatisch bedingt. Der Typ der Schluchtwaldsavanne ist ausser im heissen Tiefland besonders verbreitet in den tropischen Gebirgen, wo Höhengrasland und Höhenwald (Montane Forest) ein der Zertalung des Landes entsprechendes Vegetationsmuster bilden.

Die beiden bisher genannten Typen zeigen also ein Vegetationsgefüge: tropophile Savannengehölze — Savannengrasland — hygrophile Gehölze. Wenn man die Grassavanne heute mit Recht weithin als eine Sekundärformation durch die Wirkung des künstlichen Grasbrandes auffasst, so muss doch darauf hingewiesen werden, dass die Primärvegetation nur auf den jetzt von Grasland eingenommenen Flächen tropophiler Wald gewesen sein kann, dass dagegen die hygrophilen Waldstreifen schon in der Primärvegetation als solche vorhanden waren und heute nicht zufällige Reste der Waldzerstörung darstellen. Es wäre daher ebenso falsch anzunehmen — wie es geschehen ist —, dass die ganze Savanne ursprünglich aus hygrophilem Wald bestanden hätte.

3. u. 4. Termitenwald-Savannen

Wie ich 1936 erstmals am Beispielen aus den neu- und altweltlichen Tropen gezeigt habe, gibt es weitere Savantentypen, bei denen abseits der Täler und Flüsse fleckenhaft über die Grasflur gestreut, hygrophile, immergrüne Waldinseln auftreten, die mit grossen Nestern von Termiten (Afrika) oder Blattschneiderameisen (tropisches Amerika) zusammenfallen und auf die geologische Tätigkeit dieser staatenbildenden Insekten zurückgehen. Der rote, zähe, lehmige, oft auch harte, verkrustete Boden der Savanne (Lateritkruste, Eisenkruste) wird im Bereich der Nester gelockert, drainiert, durchlüftet, wasserdurchlässig und gedüngt,

und im Schatten der feuchten Termitenwäldchen entsteht ein milder Humusboden. Die Bevorzugung dieser Waldbosketts in bodenkundlicher und hydrologischer Beziehung ist so klar, dass in Ostafrika die Eingeborenen die Waldinseln schlagen und in kleine runde Felder verwandeln, das Grasland daneben aber nur als Weideland nutzen. Zwei ganz verschiedene Standortstypen, immergrüner Wald und baumfeindliche Grasflur wechseln hier scharf miteinander ab und auch der Grasbrand macht am Rande der Termitengehölze halt. Der Aufbau der Vegetation zeigt eine grosse Harmonie von Boden, Wasser, Pflanzen- und Tierleben und auch des wirtschaftenden Menschen. Wir haben, in der Terminologie von SUKACHEV, zwei klare biogeocöologische Systeme nebeneinander. Von den beiden in Abb. 1 unterschiedenen Möglichkeiten II und IV der Verbindung von Galeriewald-Savanne und von Schluchtwald-Savanne mit den Termitenwaldinseln, sind mir bisher nur Beispiele des zweiten Typus begegnet.

5. Dammuferwald-Savanne (oder Banco-Savanne)

Bei den bisher behandelten Beispielen waren die Grasfluren auf die Flächen ungünstiger Wasserversorgung, die hygrophilen Wälder auf die kleinen Flächen günstiger Bodenbewässerung verteilt. Es gibt aber in den tropischen Savannenlandschaften auch den umgekehrten Fall, dass ein Überschuss an Wasser in der Lage ist, den Baumwuchs auszuschliessen, nämlich in Überschwemmungsgebieten bei periodischem Klima (Seasonal Swamps). Diese Überschwemmungssavannen sind in allen tropischen Tiefländern mit Savannenklima weit verbreitet, besonders in den Aufschüttungsebenen der Ströme oberhalb ihrer Deltas, wo die Flüsse nicht in Täler eingeschnitten sind, sondern erhöht über dem Niveau der Ebene auf ihren eigenen Sedimenten als sog. „Dammflüsse“ fließen (Abb. 1, V). In der Regenzeit treten die Flüsse über die Dämme (in Südamerika „Bancos“ genannt) und setzen die seitlichen Ebenen unter Wasser, in der Trockenzeit nehmen sie das aufgestaute Wasser wieder auf und drainieren das Land. Vielfach bleiben neben den Flüssen — von

ihnen durch die Dämme getrennt — dauernde Wasserflächen, sog. „Cienagas“ (Hinterwasserseen) übrig.

In allen Fällen tragen unter diesen Bedingungen die Überschwemmungsebenen Grasvegetation, die über das Überschwemmungsniveau aufragende Bancos entlang den Flüssen immergrünen Wald (Bancowälder). Die Böden der Bancos sind ausserordentlich günstig für Waldwuchs, sandig und locker, durchlässig und durchlüftet und dabei grundwassernah. Sie liefern daher einen humusreichen Waldboden, der im Gegensatz zu den Grasfluren gerne gerodet und bebaut wird und z. B. in Ecuador den allergrössten Teil der wertvollen Kakao-böden abgibt. Die Niederungsböden daneben sind dagegen aus zähem Ton und Schlick aufgebaut und unterliegen dem allergrössten Wechsel der Jahreszeiten. In der Regenzeit sind sie aufgeweicht, in der Trockenzeit zu einer harten Tenne ausgedörrt, die in grossen Rissen aufspringt. Der Grasbrand kann dann voll zur Entfaltung kommen. In diesem jahreszeitlichen Wechsel liegt auch der Grund, warum diese Überschwemmungssavannen baum- und waldfeindlich sind, während in den Überschwemmungsniederungen des Regenwaldgebietes, wo es nie zu einer Austrocknung der Böden kommt, Sumpfwälder (Igapó, Swamp Forest) gedeihen. Es ist nach allem nicht ein einzelner Faktor wie etwa Bodenzusammensetzung, Überflutung oder Wechselklima, der den Baumwuchs in den Überschwemmungssavannen zurückdrängt sondern der ganze Komplex: wechselfeuchtes Klima, periodische Wechsel von Wasserüberschuss und Dürre, Sedimentation eines zähen, luft- und wasserdichten Tones, der sich im Rhythmus des Jahres vollsaugt und berstend zusammenzieht, schliesslich der trockenzeitliche Grasbrand, der in dem besonders hoch aufgeschossenen Savannengras der Niederung doppelt wüten kann und doppelte Wirkungen hinterlässt. In Südamerika gehören zu diesen Überflutungssavannen mit Bancowäldern z. B. die „Llanos bajos“ am Orinoco-Apuro, die „Tembladeras“ der Guayas-Ebene von Ecuador, die ganze Überschwemmungsebene der

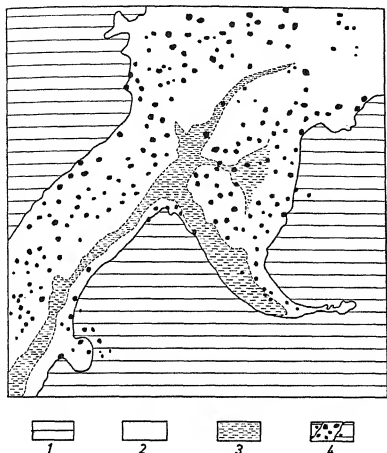


Abb. 2. Die Anordnung der edaphischen Varianten im Tloekensavannengürtel Nordrhodesiens (auf Grund einer Flugaufnahme der S. Afr. Aircraft Ltd. 160 Meilen SW von Mpika).

1. Miombowald auf trockenem Boden
2. Periodisch überschwemmtes Grasland (Dambo)
3. Sumpfsavanne (Dambosumpf)
4. Immergrüne, hygrophile Termitengehölze.

Llanos des Mamoré, die Campos des unteren Amazonas und der Insel Marajó, Gebiete am unteren Magdalenenstrom usw. In Ostafrika heißen die Überschwemmungssavannen mit schwarzen Lehm Böden „Mbugas“, in Nordrhodesien „Dambos“, in Südrhodesien „Vleis“. Sie sind nicht völlig baumfrei, sondern oft von Zwergbäumen (z. B. Beständen von Flötenakazien (Gall-acacias) bestanden.

6. Dammuferwald-Termiten-Savannen

Auch in diesen Überschwemmungssavannen können wie bei den Savannen des trockenen Bodens neben den immergrünen Waldstreifen zu Seiten der Flüsse fleckenhafte Waldinseln auftreten, die durch Termitenbauten oder Bauten der Blattschneiderameisen bedingt sind.

Das schönste Beispiel dieser Art ist die Überschwemmungssavanne des Mamoré-Gebietes, die wegen der immergrünen Waldinseln („Isla“) im Lande den Namen „Pampa isla“ führt. In Afrika gibt es sowohl in den Mbugas von Tanganyika als auch in den Dambos von Rhodesien und Katanga vortreffliche Beispiele. Die Termitenhügel bieten in der Überschwemmungssavanne der Vegetation dieselben Vorzüge hinsichtlich Luft-, Wasser- und Nährstoffhaushalt wie auf den verkrusteten Böden der Hügel-savanne.

Zum Abschluss sei die Auswertung eines Luftbildes einer ostafrikanischen Überschwemmungssavanne mit Termitenwald-Inseln („Isla-Savanne“) versucht (Abb. 2). Die weiten Felsrumpfflächen sind dort von laubwerfendem Trockenwald (Miombowald) eingenommen, der die Landschaft in den Trockensavannengürtel stellt. In den flachen Ursprungsmulden des Entwässerungssystems, die periodisch überschwemmt werden, ist der Miombowald durch offene Grasflächen (Dambos) ersetzt. Der Rand der Dambos gegen den Trockenwald ist scharf gezeichnet durch die Überschwemmungsgrenze. Innerhalb der Dambos verläuft mit unscharfer Grenze, im Luftbild durch die dunkleren Tönungen erkennbar, ein bachbettloser Entwässerungstreifen, in dem die Überflutung und die Bodenfeuchtigkeit besonders stark und lange wirksam sind, sodass Sumpfsavanne entsteht. Über das Dambo-Grasland sind die dunklen Flecken der Termitenwaldinseln (Isla-Gehölze) unregelmäßig gestreut, sie liegen in der normalen Überschwemmungssavanne und greifen nur an wenigen Stellen randlich auf den Miombowald oder auch auf die Sumpfsavanne über.

Im Raume des Bildes sind also vier standortliche Vegetationstypen des klimatisch einheitlichen Trockensavannengebietes auf das Deutlichste unterschieden, räumlich klar abgrenzbar und mit dem physiographischen Aufbau des Landes in Verbindung stehend: 1. laubwerfender Miombowald auf trockenem, nichtüberschwemmtem Boden (nach Forschungen von CH. R. ROBBINS (1934) roter Lehm oder Lateritlehmboden), dem regelmäßigen Grasbrand

unterliegend, also ein „Fire Climax“. 2. Überschwemmungssavanne (Dambo-Grasland), in der Regenzeit überschwemmt, in der Trockenzeit gebrannt, mit zähem, grauem, humosem Tonboden, also eine „Flood and Fire Climax“. 3. Sumpfsavanne mit ständiger Feuchtigkeit (Dambo-Sumpf), nicht oder nur selten gebrannt, mit sehr nassem, schwarzem Humustonboden. 4. Hygrophile, immergrüne Gehölzinseln auf Termitenhügeln mit gut durchlüftetem, durchlässigem und gedüngtem Boden, nicht dem Grasbrand unterworfen — ein Biotop, bei dem die Tierwelt erst die Voraussetzungen für die Vegetation erzeugt.

Die Analyse der vier verschiedenen Vegetationstypen, die an dieser Stelle im Gelände noch nicht durchgeführt ist, müsste mit den Methoden der Pflanzensoziologie erfolgen. Nach Erfahrungen in benachbarten Gebieten würden sich voraussichtlich ergeben: 1. eine *Brachystegia-Berlinia-Uapaca*-Assoziation für den Miombowald; 2. eine Assoziation von Gräsern der Gattungen *Andropogon*, *Panicum*, *Paspalum*, *Pennisetum*, *Hyparrhenia* etc. und eingestreuten Stauden und Kräutern für die normale Überschwemmungs-Grassavanne; 3. eine Sumpfgesellschaft (*Hydroseral Community*) mit Elefantengras (*Pennisetum purpureum*) oder einer noch feuchteren Gesellschaft mit *Cyperus*- und *Typha*-Arten; 4. eine immergrüne Feuchtwald-Assoziation mit *Euclea Kellau*, *Carissa edulis*, *Myrsine africana*, *Clerodendron* etc. als Bäumen und *Gloriosa*, *Asparagus*, *Rhoicissus* etc. als Lianen auf den Termitenhügeln.

Im Hinblick auf die Diskussionen der letzten Tage möchte ich auf Grund eigener Erfahrungen über die Methode und die Rolle der pflanzengeographischen, pflanzensoziologischen und pflanzenökologischen Arbeitsrichtungen folgendes sagen. Für die Untersuchung der Vegetationsverhältnisse eines Gebietes sind alle drei Methoden notwendig. Auch die Reihenfolge der Untersuchung ist durch das Objekt und die Aufgabe eindeutig vorgeschrieben. Es handelt sich um vier Aufgaben: 1. Die Feststellung der standörtlichen Typen aus der ersten Zusammenschau von Pflanzenkleid und Landschafts-

aufbau, also die pflanzen-topographische Gliederung, die zu einer Ausscheidung und Abgrenzung der nebeneinander vorkommenden edaphischen Varianten der Vegetation führt. 2. Die pflanzensoziologische Bestandsaufnahme der einzelnen Einheiten, für die verschiedene Methoden in Gebrauch sind. 3. Die ökologische Analyse der Wachstumsbedingungen der einzelnen Einheiten (Boden und Bodenprofil, Bodenwasser, Mikroklima etc.), soweit möglich messend und experimentell. 4. Die Gruppierung der festgestellten Vegetationseinheiten. Bei diesem letzten Akt sind zwei Wege möglich: a) die Aufstellung eines pflanzensoziologischen Systems, auf floristischer Grundlage, wobei die in der Natur auf engstem Raum nebeneinander vorkommenden Einheiten in ganz verschiedene Assoziationen, Formationen, auch in verschiedene Verbände und Klassen eingereiht werden. Die räumliche Gruppierung in der Natur wird dabei fallen gelassen. Ich persönlich empfinde in dieser soziologischen Gruppierung eine künstliche Klassifikation, ein künstliches System. b) Die räumlich-standörtliche Gruppierung eines pflanzengeographischen Systems, wobei die in der Natur nebeneinander vorkommenden Typen als edaphische Varianten eines klimatischen Vegetationstypus aufgefasst und zu einem Komplex von Assoziationen und Formationen zusammengekommen werden. Die in einer Karte oder wenigstens in Skizzen charakteristischer Landschaftsausschnitte festzuhaltende Anordnung der Assoziation in Verbindung mit den physiographischen Verhältnissen ergibt das Vegetationsgefüge (vegetation pattern) als Ausdruck der natürlichen Gruppierung der Vegetation.

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Discussion

H. WALTER: TROLL fasst den Begriff vom geographischen Standpunkt auf. Es ist ein Landschaftsbegriff, ein Makromosaik von zwei ganz verschiedenen Standorten und Gesellschaften. Dem gegenüber ist die Dornbusch-savanne standörtlich und soziologisch einheitlich. Darin ist eine Gefahr des Savannenbegriffs zu sehen, der Begriff ist nicht einheitlich.

M. SCHWICKERATH erörterte im Anschluss an die Ausführungen von DU RIETZ die Verknüpfung und Ähnlichkeit von Verbänden und Ordnungen mit den Landschaftseinheiten.

Verbände und Ordnungen sind eine rein begriffliche Weiterbildung der soziologischen Grundeinheit, die nichts mit landschaftsgeographischen Einheiten zu tun hat. Natürlich besteht eine Brücke, die aber auf anderem Gebiet liegt. Die Sukzessionsfolgen einer bestimmten Örtlichkeit mit ihrem Terminalstadium oder Klimax bilden ein ganz bestimmtes Assoziationsgefüge, einen Assoziationskomplex. Dieses Assoziationsgefüge ist identisch mit dem Landschaftselement im Sinne TROLLS, das erste Mal ausgedrückt in der Sprache des Soziologen, das zweite Mal ausgedrückt in der Sprache des Landschaftsgeographen. Die Landschaftsbeurteilung ist dann weiterhin eine landschaftsgeographische Angelegenheit.

C. TROLL: Zur Methode: Es besteht kein nennenswerter Unterschied in der Methode der pflanzensoziologischen und ökologisch-pflanzengeographischen Forschung. Der Unterschied betrifft die Darstellung. Um die Vegetation der Erde beschreiben zu können, kann ich noch für Jahrzehnte nur die geographisch-ökologische Methode anwenden, die soziologische würde noch jahrzehntelange Vorarbeit von Generationen erfordern.

Begriff Savanne: Ich spreche nur von Savannengürteln und in jedem Gürtel von verschiedenen Typen von Savannen-Grasland und Savannengehölzen. Auch den Dorngraslandgürtel in die Savannengürtel aufzunehmen, entspricht den neueren Vorschlägen von Bota-

nikern und Geographen (z. B. JAEGER). Eine „Savanne“ schlechthin gibt es nicht.

Primär-Savanne: Die hygrophilen Waldinseln unterliegen nicht dem Savannenbrand, sondern nur die tropophilen Formationen (Savannengrasland und Savannengehölze). Die selektive Wirkung des Feuers ist beträchtlich, die Physiognomie der Vegetation ist wesentlich vom Feuer beherrscht. Aber die Vegetation ohne Wirkung des Feuers werden wir wohl nie erforschen können. Sie ist vielleicht nie vorhanden gewesen. Denn auch eine gegen den jährlichen künstlichen Savannenbrand geschützte Vegetation unterliegt in langen Zeitabständen der natürlichen Blitzzündung. Man könnte daher unterscheiden zwischen einer dem regelmässigen künstlichen Brand unterworfenen und einer nur von den seltenen natürlichen Bränden beeinflussten Savannenvegetation. Die Zerstörung der hygrophilen Wälder erfolgt nur durch die Rodung des Waldes und die „shifting cultivation“. Die so entstehenden Sekundärformationen sind in Ostafrika und in den andinen Bergwäldern vor allem *Pteridium aquilinum*-Assoziationen.

Brandvegetation ausserhalb der Tropen: Auch in Mitteleuropa gibt es Grasbrand und regelmässig gebrannte Grasvegetation. Es sind die Assoziationen von *Brachypodium pinnatum*, die künstlich entstehen, wo in Grasheiden das Aufkommen von *Prunus spinosa* und anderen Gehölzen durch regelmässiges Brennen im Spätwinter verhindert wird, besonders durch Schäfer. Die „Fire-Climax“ von *Brachypodium pinnatum* entspricht vollkommen den besprochenen tropischen Beispielen.

F. RAWITSCHER, G. E. DU RIETZ, H. HUMBERT und H. BOYKO also took part in the discussion.

M. ZOHARY (Jerusalem)

Phytogeographical Problems of the Near-East Countries

(1) The delimitation of the Mediterranean region (in the sense of GRISEBACH,

BOISSIER, etc., i. e., restricted to areas with true Mediterranean conditions) toward the adjacent Irano-Turanian region has been carried out on the following criteria:

(a) Floristical: Towards East and South there is a sudden drop in the number of Mediterranean species of high vegetational value and a corresponding rise in number of Irano-Turanian species.

(b) Vegetational: The Mediterranean region, except at alpine altitudes, is characterized by arboreal climaxes, whereas in the Irano-Turanian territory no such climaxes are found.

(c) Ecological: The isohyete of 350 mm roughly coincides with the boundary of the Mediterranean region in the East and South.

On the map shown, within the Mediterranean territory a narrow transition belt is included, distinguished by high percentage of Irano-Turanian plants, penetrating into Mediterranean plant communities.

(2) Mediterranean enclaves in the midst of the Irano-Turanian and Saharo-Sindian regions at a considerable distance from the parent Mediterranean territory are relic areas of Mediterranean vegetation dating from a more humid period (Pluvial A of the Pleistocene) and preserved in particularly favourable habitats.

(3) The southernmost boundary of the Mediterranean region in the East runs south of Petra (alpine heights) where the *Quercus calliprinos*-*Juniperus phoenicea* forest and a few stands of *Cupressus sempervirens* are found.

(4) The *Pistacia atlantica* belt borders the Mediterranean territory on the East and extends into it where primary vegetation has been destroyed.

(5) The Sinaitic-Lybian gap. Though the Mediterranean coast is surrounded by Mediterranean vegetation, there is a gap between Southern Palestine and Cyrenaica, owing to low rainfall. This gap impedes the interchange of Mediterranean species between Asia and Africa. The absence of many East Mediterranean trees in North Africa leads to an

assumption that the omni-Mediterranean element reached Africa direct from the North.

(6) Saharo-Sindian penetrations into and shifting of vegetational zones within the Mediterranean region were caused by:

(a) Edaphical conditions: The coastal dunes of Palestine, with prevailing typical Mediterranean climate, are penetrated by Saharo-Sindian species as far as Beirut.

(b) Destruction of woody climaxes: Saharo-Sindian, Irano-Turanian and Sudano-Decanian species occupied vast stretches in Eu-Mediterranean areas, some of them forming pseudo-climax.

(7) Pre-Pliocene tropical relics. Most of the forty tropical species in Palestine are relics of a period when the country was detached from the North Mediterranean by the Thetis and formed the Northern fringe of a tropical domain.

F. RAWITSCHER (São Paulo)

showed the pictures belonging to his paper on Climax and Pseudoclimax Vegetation in the Tropics (South America) read on July 14th, p. m.

I. REICHERT (Rehovot)

Steppes and Deserts in the Eastern Holarctis in Relation to Lichens

The xeric vegetation units in the eastern Holoarctis are chiefly concentrated in three regions: Arctic, Mediterranean, and Irano-Turanian, occurring less frequently in the intermediate Eurosiberian region. The arctic region harbours the xerofrigid plant formations called Tundra. Outstanding are lichens of the genus *Cladonia*, section *Cladina*.

The Mediterranean and Irano-Turanian may be divided into two sections:

(1) Plateaux, rising in the west from 300 and reaching 2000-3000 m in the east. Here are located the real xerothermic steppes, characterized especially by *Artemisia*, the characteristic lichens of which are the various species of the genus *Diploschistes*. In the east, as an adapta-

tion to xerophytic conditions, these species form large thick patches, thus counteracting the desiccation of the soil and of the lichens themselves. Toward the west, these patches decrease, both in size and in number.

(2) Plains and lower elevations of the southern regions present xerothermic deserts, characterized by *Zygophyllaceae*. No *Diploschistes* occurs. The characteristic lichens are *Ramalina* spp. of the *maciformis* group, showing special xerophytic adaptations.

In the Eurosiberian region genuine steppes are found only in the east in the South Russian area, where *Diploschistes terrestris* is characteristic; in the west, *albissima*, *cretacea* and *ocellata* are common. Especially interesting is the species *Diploschistes bryophilus* which lives parasitically chiefly on *Cladonia*, thus forming a "plant-bridge" between *Diploschistes* and *Cladonia*.

With respect to alpine vegetation: in the Arctic, the high mountains are covered with ice; in the Eurosiberian region, the alpine areas are covered by mesothermic plants with xerophytic adaptations; in the Irano-Turanian, the alpine area is characterized by extremely xerophytic plants such as *Astragalus tragacantha*, etc. Special xerophytic lichens from the *Lecanora esculenta* group (Manna lichens) are characteristic for the Irano-Turanian and South-west Mediterranean Atlas Mts. and are not found either in Eastern Asia or in the high mountains of Europe.

A paleo-historical analysis leads to the following considerations:

(1) The *Cladonia* spp. of the arctic tundras originated in the north, existing there in the Tertiary period. With the onset of glaciation they moved to the south and east, returning to the north after the ice retreated.

(2) The lichen components of the southern steppes, *Diploschistes* spp., originated in the Paleoafrican area of Southern Africa from whence, together with many other xerophytic plant groups, they emigrated to Central Asia.

(3) The alpine *Esculenta* lichen vegetation of the Irano-Turanian and the Atlas Mts. must have originated in the high mountains of the

Irano-Turanian region during the Miocene period when the eastern part of the Thetis Sea, in Central Asia, dried up and the *esculenta* and *tragacantha* spp. assumed their extremely xerophytic transformation.

The *esculenta* and *tragacantha* vegetation migrated from Central Asia to the west and then to the south, but whereas the *tragacantha* stopped at the Balkans, the *esculenta* migrated to North Africa through the ancient Italic Bridge. This is also the reason why no *esculenta* are to be found in the Alpine regions of the Alps and Carpathians.

LUCY B. MOORE (Wellington)

Mat Plants of the Genus *Raoulia* as Weeds in Pastoral Land

Mat plants of several species of the Composite genus *Raoulia* are normal components of the tussock grassland that is used for grazing range stock in the South Island of New Zealand. When this vegetation is depleted in low rainfall areas by fire or otherwise, some of these and other species of *Raoulia* colonize the ground left bare between the bunch grasses. Eventually, with further abuse, the larger grasses may disappear and mat plants of two or three species of *Raoulia* can then occupy the land almost exclusively. Seeds of tussock grassland species germinate more readily in *Raoulia* mats than on bare exposed soil, but such seedlings can remain alive without change of size for several years, and quite commonly do not develop into adult plants at all.

In Marlborough the *Raoulia lutescens* community has been observed to show little change or even growth of its components over a period of six years, in spite of minimum grazing or erosion, without fire, and with ample sources of grassland seeds nearby. Here it must be regarded as a permanent vegetation. Whereas *Raoulia* mats on newly formed river terraces are important members in the succession from bare shingle to tussock grassland, in other situations where they occupy areas previously carrying a low tussock community, they must,

in some cases, be regarded not as weeds but as dominants in a climax vegetation under present conditions.

This permanent change following a catastrophic elimination of primitive vegetation is considered in relation to evidence for recent climatic change provided by CRANWELL and VON POST from pollen analysis studies, by RAESIDE from a consideration of soils, and by HOLLOWAY from investigations in *Nothofagus* forests, all working 200–300 miles south of the district in which the observations here reported were made.

H. BOYKO (Hakirya)

Regeneration Problems of the Vegetation in Arid Zones

Everywhere in the broad, arid belts on both sides of the equator we can observe the various degrees of destruction, starting e.g. with the remnants of a *Lauretum nobilis* in the Maquis of the North-Mediterranean area to the *Anabasisideta articulatae* on the borders of the climatically conditioned desert.

The primary desert area, however, is astonishingly small, and we can find out the anthropogenic origin of enormous stretches of deserts and semideserts with the aid of close plant-sociological investigations.

Their rehabilitation has always presented the greatest difficulties. The main cause of these difficulties lies in the fact that we are concerned in most of the cases with the utmost limits of the ecological amplitudes of the single species and that, therefore, otherwise small and insignificant factors and fluctuations rise to life-decisive prominence. The study of the micro-conditions in these areas is therefore the first postulate for every afforestation and every rehabilitation of the vegetation altogether.

The "Geo-Ecological Law of Distribution" and the knowledge of climatic extremes as decisive factors for plant distribution provide us

with a sound basis for the application of these studies.

As another postulate the investigation on climax-vegetation can be looked upon. It is shown by examples that this can be reconstructed in spite of the terrific destruction of the original vegetation.

A further substantial help for this reconstruction is provided by the method of the shifts in amplitude which show, in the case of a number of species, a mathematically definable regularity (see Chron. Bot. IX/2–3: 86–88). For these purposes the necessity arises of erecting a worldwide net of ecological observation stations with standardized methods and a close international cooperation. It seems to me to be one of the most important tasks of the new Commission for Applied Ecology to create the organisation of such a network.

Closely connected with the questions of rehabilitation are the many-sided problems which present themselves in the preparation and execution of large hydraulic-engineering projects in arid areas. With plantsociological methods one can detect, for instance, besides water percolation through soil strata, also crevices and geological dislocations hidden by soil layers up to a depth of 100 m and more. This new method, particularly important for projects of valley dams, is shown with the help of practical examples.

The meteorological data in arid zones are mostly very poor; here too a method has been devised to determine more exactly the climatic data, especially the precipitation, with the help of exact plantsociological analyses and the shifts in amplitudes, to a quantitative measure. (Examples: *Laurus nobilis*, *Artemisia herba-alba*, etc.). The exactitude will most probably not lag behind the measurements by totalisators for rainfalls. The benefit of this method is that thereby we receive biological standards for the climate, a fact which is especially important for its application in forestry and agricultural work.

SESSION 11

July 20th, 1—2.30 p. m.

Chairman: F. R. BHARUCHA, Recorders: G. E. DU RIETZ and H. SJÖRS

SUBJECT:

Various Papers

HANS LUTHER (Helsingfors)

Höhere Wasservegetation und Standortsfaktoren in der Ostsee¹

Beim Untersuchen der Standortsfaktoren der Pflanzen kann man zwei Wege einschlagen: 1. Man wählt einen bestimmten Faktor oder Faktorkomplex aus, der unter Ausschaltung übriger Faktorkomplexe untersucht wird. Positive Befunde sagen hierbei aus, dass die Verhältnisse am Standort der Pflanze zusagen, negative Befunde beweisen keineswegs ohne weiteres dass gerade der untersuchte Faktor am Fehlen der Pflanze Schuld ist. 2. Man wählt Standorte aus, die in Bezug auf bestimmte Faktoren homogen sind. Diese Faktoren scheiden aus der Betrachtung aus und der ganze Problemkomplex lässt sich leichter analysieren. Diese Methode ist viel zeitraubender als die erste, dürfte aber besser die wirklichen Standortsansprüche der Pflanze klarlegen.

Die Ostsee ist als Brackwassergebiet einzigartig in der Welt. Hier findet unter gleichzeitiger Ausschaltung der Gezeiten eine schrittweise Aussüßung des Meerwassers bis zu völlig süßem Wasser statt. Dazu treten die übrigen Standortsfaktoren in den mosaikartig wechselnden Schärengebieten in den mannigfaltigsten Kombinationen auf, was uns gewissermassen ermöglicht aus einem genügend grossen Material den jeweils die Verbreitung bestimmenden Faktor auszulesen.

Das in der Nähe der Südspitze Finnlands gelegene 40 km lange Pojowiek-Gebiet ist in Bezug

auf Salinitätsabstufungen etwa den Finnischen und Bottnischen Meerbusen gleich und ermöglicht uns auf beschränktem Raum die wasserchemisch bedingten Abstufungen der Wasserpflanzen zu studieren. Infolge der mannigfachen Kombination der Standortsfaktoren lassen sich Licht, Wärme, Wassertiefe, Exposition, Bodenart, Konkurrenz und die Verbreitungsbiologie der Pflanzen als verbreitungsbegrenzende Faktoren grösstenteils ausschalten.

Die Salinitätsgrenzen der Arten verschieben sich beim Einwärtsgehen in die Ostsee, die Grenzen der halophilen Arten und der Süßwasserarten nähern sich einander. Die Salinität wird in brackwasserökologischen Arbeiten meistens als abstrakte Mittelwerte ausgedrückt, während die Reaktion der Pflanze in der Tat durch die Schwingungsamplitude und die Schwingungsfrequenz des Salzgehaltes bestimmt wird. Diese Schwingungen sind ausserhalb der Ostsee gross, weshalb dort die Salinitätsamplituden der Arten eng sind, in der inneren Ostsee sind die Schwingungen unbedeutend und die Amplituden deshalb weiter. Teilen wir die Wasserpflanzen nach ihrer Salinitätstoleranz in das übliche Spektrum ein so müssen wir eine gleitende Skala für die Grenzen der Stufen verwenden. So rückt die obere Grenze der oligohalinen Stufe, die in salzigeren Gebieten bei 1,8 ‰ gezogen wird, in der inneren Ostsee bis 3 ‰ hinauf.

Durch lakustrine Aussüßungsfaktoren bedingt sind die Innengrenzen einiger alkaliphilen Süßwasserpflanzen, die im elektrolytenarmen, oft sauren Urgesteinswasser Fennoskandiens äusserst selten sind oder fehlen. Teilweise erreichen diese Arten schon vor dem Flussmündungs-

¹ Die hier ganz kurz referierte Arbeit ist in *Acta Bot. Fenn.*, 49-50 (1951) erschienen.

gebiet ihre Innengrenzen und zeigen hierdurch deutlich an, dass ihr Fehlen im Urgesteinswasser wasserchemisch bedingt ist.

Discussion

J. IVERSEN et H. LUTHER took part in the discussion.

J. TROCHAIN (Brazzaville)

Les types de végétation en Afrique Noire Française

Leur caractérisation

Cette note s'intègre dans les sujets d'étude mis à l'ordre du jour par la Section de Géographie botanique du VI^e Congrès (Amsterdam 1935). Elle complète et précise celle que nous publions en 1946.

Types de végétation: Grands ensembles végétaux qui impriment au paysage une physiologie particulière parce qu'ils résultent de l'accumulation d'espèces végétales, spécifiquement variées mais appartenant, en grande majorité, à une même forme biologique qui est ainsi dominante. Cette forme biologique est sous la dépendance des facteurs du milieu de sorte qu'à la notion primitive de «formation», terme à rejeter de la langue française, se substitue celle, soit plus, soit moins compréhensive, mais toujours écologique, de Type de Végétation.

La critère physiologique est à la base du système élaboré. Mais tout de suite d'autres caractéristiques: écologiques, biologiques, floristiques, biotiques, géographiques, topographiques y sont introduites pour permettre la distinction d'unités définies et hiérarchisées et laisser la place à éventuelles subdivisions. Nulle inféodation de ces éléments les uns par rapport aux autres ne paraît possible: ils doivent rester aussi intimement entremêlés qu'ils le sont dans la Nature.

La distinction des Types de Végétation, qui correspondent chacun à une écologie donnée, est indispensable dans ces pays botaniquement peu connus de l'Afrique Noire Française. Quand

ultérieurement on les aura, complètement et partout, disséqués en groupements végétaux encore peu, ou mal, délimités floristiquement et spatialement, la notion de Types de Végétation ne disparaîtra pas pour autant. Elle servira alors de cadre général ou assise des recherches de détail et elle permettra les vues d'ensemble.

Le tableau synoptique présenté ne pouvant être encore résumé il est préférable d'attirer l'attention sur quelques définitions générales:

— Pseudosteppe: forme biologique herbacée ou demi-ligneuse dominante. Peuplement ouvert, plus ou moins parsemé d'arbrisseaux avec une seule période de repos (sécheresse).

La (ou le) steppe, peuplement fermé à deux périodes annuelles de repos (froid et sécheresse) n'existe donc pas en Afrique noire française.

— Savane: peuplement herbacé dominant parsemé d'arbustes ou d'arbres isolés. Dans son sens primitif la savane correspond à cette définition et non à celle d'étendue herbeuse entièrement dépourvue de toute végétation ligneuse. Ceci c'est la (ou le) pseudosteppe.

— Savane arborée et savane forestière: peuplement arboré ouvert dominant, avec tapis herbacé saisonnier important.

— Brousse: peuplement arbustif fermé, à peu près dépourvu de tapis herbacé.

— Forêt: peuplement arboré fermé, sans tapis herbacé important.

— Futaie caducifoliée des pays à déficit de saturation important durant la saison sèche: forêt claire.

— Futaie sempervirente, ou partiellement et courtement caducifoliée, des pays à déficit de saturation toujours faible: forêt dense.

Des subdivisions de ces grandes rubriques sont prévues et les équivalences de ces termes avec ceux employés par d'autres Auteurs (BURTT-DAVY, FRANCKE, MANGENOT, AUBREVILLE, PITOT, SCHNELL) sont établies.

Aux termes proposés et définis — qui traduisent un état de fait actuel et ne préjugent pas du climat — d'autres précisions peuvent être apportées en ajoutant le nom de la, ou des, espèces dominantes ou codominantes (ce qui permet de faire apparaître les différentes stra-

tes) ou encore en adjoignant un qualificatif chorologique.

Le rapport in-extenso sera publié dans le N° 2 du Bulletin de l'Institut d'Etudes Central-africaines de Brazzaville (A. E. F.).

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F. R. BHARUCHA and P. J. DUBASH
(Bombay)

The Problem of Nitrophily

From the definitions advanced by various authors, we find that no one of them definitely and explicitly mentions whether a high concentration of nitrates is *absolutely necessary* to a nitrophilous plant or whether it can *merely endure* nitrates in high concentrations. The confusion is due to the fact that no one of them has realized that there are degrees in nitrophily. The whole range of nitrophily stretches from plants absolutely restricted to nitrates to those indifferent to them and yet occurring in nitrate habitats. These plants can thus be classified in the same way as UNGER classified plants with regard to lime and silica, namely, (i) indifferent to such soils, (ii) partial

to such soils and (iii) restricted to such soils. Thus, whether nitrates are necessary to a nitrophilous plant or not, depends upon what we mean by a nitrophilous plant and upon its place in classification.

We have, therefore, set out along a new line of approach, viz. a study of the nitrophilous vegetation according to both chemical and statistical data. The results have been synthesized according to a new formula proposed by us and from its use we have produced a list of a few Indian nitrophilous plants and have graded them according to their nitrophily and indicator value. Some of them are so specific about their habitat conditions that they may be termed the characteristic species of the nitrophilous association.

Since nitrophily does not merely depend upon the capacity of the plant to accumulate nitrates but also to a large extent upon its indicator value, in other words upon the frequency of its presence in high-nitrate habitats, we have introduced into the formula three factors, namely, the frequency of the species, the constancy of the nitrates present in the samples taken, and finally the average nitrate content of the plants.

We have found that working with this formula, the results concur with the statistical data gathered of the plants of the association by using BRAUN-BLANQUET's method, which amply supports the concept of the characteristic species of a plant association as defined by the Zürich-Montpellier school of Plant Sociology.

The paper was read by R. R. BARUCHA.

PAPERS DELIVERED BUT NOT READ OWING TO LACK OF TIME

W. R. ACCORSI (São Paulo)

Biology and Ecology of the Podostemonaceae of the Piracicaba Fall

The author presents the results of his studies concerning the biology and ecology of the Podostemonaceae under observation since 1943 in the Piracicaba Fall (State of São Paulo,

Brazil). They are represented by four species which have a limited local distribution in consequence of their specialized adaptation to the varying ecological characteristics of the current besides their general adaptation to submerged habitats. Their distribution is the following: (1) *Apinagia Accorsii* Toledo, on rocks situated just within the water fall where veloc-

ity of the current and aeration of the water are very high; (2) *Mniopsis Glazioviana* Warmg. and *Tristicha hymnoides* (St. Hil.) Spreng. var. *Hilarii* Tul., on rocks at some distance (100 m more or less) upstream; (3) *Mourera aspera* (Bong.) Tul., on rocks between 300 m and 800 m above the water fall.

The biological cycle is divided into two phases in accordance with ecological factors:

A. — During the flood period (October until April) the plants stay completely under water, expanding and increasing their vegetative organs by means of: (1) stolons with vegetative buds and with regeneration of the remaining rhizomes in *Apinagia Accorsii* and *Mourera aspera*; (2) roots with vegetative buds and budding of active branches in *Mniopsis Glazioviana*; (3) stolons with vegetative buds and budding of active branches in *Tristicha hymnoides*.

B. — During the dry period (May until October) the plants emerge above the water level and flower and produce fruits, exclusively in contact with air.

The vegetative system above the water level dries up and dies. However, the fruits attach themselves with their pedicels to the rocky substratum, being able to support later on the great intensity of the first currents, following the first heavy rains of the next rainy season. Due to the irregular configuration of the hard river bed (diabase rocks), some plants remain submerged even during the dry period, continuing to grow, while semiexposed plants produce flowers and fruits rapidly in their parts in contact with the atmosphere.

Propagation by seeds has been studied in detail in *Apinagia Accorsii* and *Mniopsis Glazioviana*. The germination begins during the flood period following the first rains and may occur in the following places: (a) placenta of partially open fruit; (b) external and internal walls of the open capsules; (c) pedicels of the fruits; (d) remains of branches, rhizomes, etc.; (e) organic residues accumulated in water holes within the fall. Seeds adhere to the above substrata by means of a mucilage resulting from the

transformation of their external integuments, when in contact with water. The very small seedlings, which can be studied only under the microscope, have no main root, but a large number of root hairs develop around the hypocotyl, whose principal function seems to be fixation of the seedlings to the substratum.

The transfer of the young plants, which develop in the placentas, capsules and fruit pedicels, etc., to the rocks takes place when they have become too heavy for the pedicels to carry their weight. Their attachment to the rocks is made by means of special fixation cells and hapters.

If the body of the plants is completely dead at the end of the dry season, only the fruits remain sticking on the rocks in contact with the atmosphere and the surviving of the species in its habitat depends exclusively on the germination of seeds on the above mentioned substrata, especially the fruit capsule, which constitutes the best means for the protection of the seedlings in extreme conditions of dry heat. Only exceptionally some plants survive in a few water pockets continuously kept full by the weak remaining current.

CLAIR A. BROWN (Baton Rouge, La.) *Studies on the Isolated Prairies of Louisiana*

The presence of prairies in a region climatically capable of supporting a forest vegetation is especially interesting. The prairies under discussion have been termed isolated prairies because they occur outside of the general prairie region of southwestern Louisiana.

Most of these natural treeless areas have been known since the early explorations of the State. More than 75 have been recorded and over 60 of these have been visited by the writer in the past few years.

In general these are dry prairies in contrast to our marshland prairies, and fall into two groups: first, those with yellow soils; and second, those with black soils. These prairie spots vary in age from those on the recent floodplain to those on the Tertiary outcrops. Usually, the

black soil prairies are on the Tertiary exposures, whereas the yellow soil prairies are on the Pleistocene terraces. Most of those isolated prairies have a common soil feature. There is an impervious layer about 6 to 9 inches below the surface. Below this layer the soil is more pervious and contains calcareous concretions. This layer is not the hard pan proper. It prevents the downward percolation of water and likewise prevents the upward movement of water by capillarity. This impervious layer makes it possible to grow rice over most of the prairie region of southwestern Louisiana.

It is not possible to present the flora of an undisturbed prairie as all of them appear to have been cultivated at one time or another. The flora of the black soils is quite similar from prairie to prairie, whereas the flora of the yellow soils is more diverse. In general the flora of these prairies is similar to that of the respective adjoining areas except for the absence of trees and the greater abundance of certain grasses and herbs. The yellow soil prairies have a mesic spring flora and a xeric fall flora. Many of the plants present on these isolated prairies are typical for the tall grass prairies of the central United States.

One must conclude that something in the origin of these areas has retarded or prevented their invasion by forest vegetation. Several appear to be old lake beds. This concept has been supported by the study of a group of prairies on the recent flood plain which are developing from a lake that is diminishing in size. Most of them are not of lacustrine origin.

A. FOURY (Rabat)

Contribution à l'étude de la flore des Hauts-Plateaux du Maroc Oriental

Les Hauts-Plateaux du Maroc Oriental, ou Dahra, constituent le prolongement de la Meseta oranaise (1). Ils sont limités au Nord par la Gada de Debdon surplombant la plaine de Tafraça; les massifs des Beni-bou-Zeggon, de Zekkara et des Beni-Yala qui dominent les plaines de Djefira et des Angads. Au Sud, une

zone de plissements atteignant 2.000 mètres unit le Grand-Atlas oriental à l'Atlas saharien d'Algérie et englobe la haute-plaine de Tamlelt. Le climat de toute cette région élevée est continental et sévère: froid en hiver, où la température s'abaisse au-dessous de 0°C, avec de la neige et de la grêle chaque année; très chaud et sec en été, avec plus de 40°C. Les vents y sont violents. La pluviométrie, d'après la carte de M. G. ROUX (2), est comprise entre 100 et 200 mm, sauf dans la région montagneuse du Nord et une petite tache autour de Tendrara, qui sont plus arrosées. Cette moyenne annuelle étant basée sur les observations effectuées de 1926 à 1940.

Nos connaissances sur la Flore des Hauts-Plateaux marocains ont été excellemment résumées par M. le Professeur L. EMBERGER dans son «Aperçu général sur la végétation du Maroc» (3) et deux grandes associations climatiques y ont été distinguées: la steppe à Halfa et l'artemisia à Chih.

A ce propos, M. EMBERGER s'exprimait ainsi:

«L'association de l'Halfa est encore à déterminer. La pluviosité étant très irrégulière d'une année à l'autre, il faudrait faire des relevés suivis pendant un certain nombre d'années. Certaines années sèches, la flore des Hauts-Plateaux est désespérément pauvre, et l'Halfa en est alors l'espèce exclusive; d'autrefois, quand il a plu, elle est d'une grande richesse. L'artemisia est toujours pauvre.»

Ayant eu la possibilité de parcourir les régions des Hauts-Plateaux au printemps 1948, pour examiner l'état des pâturages et leur valeur fourragère, j'ai pu faire des observations sur la composition des principales associations végétales.

Il convient tout d'abord de noter que l'année 1948 peut être considérée comme une année de pluviométrie normale pour la région succédant à des années sèches. Entre la zone désertique du Sud, limitée par l'isohyète de 100 mm suivant la ligne approximative Figuig-Bou Denib, et la zone montagneuse au Nord de la ligne El Ateuf-El Harcha, où la pluviométrie supérieure à 200 mm et l'altitude permettent la forêt, s'étendent

les espaces monotones des Hauts-Plateaux proprement dits.

L'arbre n'existe que dans les vallées où l'on rencontre : *Tamarix*, *Nerium oleander* L., *Retama sphaerocarpa* (L.) Boissier.

Des taches limitées de végétation plus ou moins halophile se trouvent près de Mengèb, à Berguent, près d'Ain Merija. Les plantes récoltées comprennent : *Atriplex Halimus* L., *Sal-sola vermiculata* L., *Suaeda mollis* (Desf.) Del., *Suaeda fruticosa* (L.) Forssk., *Aizoon hispanicum* L., *Lygeum spartum* L.

La végétation de la partie restante peut être schématiquement résumée comme suit :

1° — l'association de l'Halfa occupe deux grandes nappes à contours irréguliers, celle du Nord est divisée en deux parties dont l'une est reliée aux forêts de la Gada de Debdou et dont l'autre continue les nappes de l'Oranie septentrionale; celle du Sud s'étend au nord du Chott Tigri et de la région de Bou-Arfa, elle recouvre notamment le Jebel Tendirra.

2° — l'artemisaie occupe, entre ces deux ensembles, toute la cuvette centrale de la région des Hauts-Plateaux entre Tendirra et Berguent.

A — L'association de l'Halfa

Les nappes alfatières sont surtout constituées par l'Alfa ou Halfa (*Stipa tenacissima* L.) plante à cellulose, mais qui, au point de vue fourrager, ne constitue qu'un aliment de disette. A côté de cette graminée, on trouve des espèces du genre *Stipa* à bonne valeur nutritive (*Stipa barbata* Desf., *Stipa parviflora* Desf., *Stipa retorta* Cavan.) *Cynodon Dactylon* (L.) Pers.; *Crotandia menphythica* (Spreng.) Benth., excellente plante fourragère très abondante dans les pâturages voisins du Chott Tigri; *Dactylis glomerata* L., *Lamarkia aurea* (L.) Moench; *Schismus barbatus* (L.) Thell.; *Bromus rubens* L.; *Eremopyrum orientale* (L.) Jaub. et Spach; *Lolium rigidum* Gaud.; *Hordeum murinum* L.; *Lygeum spartum* L. existe surtout dans les zones de passage à l'artemisaie. Parmi les Caryophyllacées les Paroniques sont abondantes (*Paronychia arabica* (L.) DC., *Paronychia argentea* Lamk., *Paronychia chlorothyrsa* Murbeck); parmi

les Ranunculacées *Ceratocephalus falcatus* (L.) Pers., *Adonis dentata* D. C. Dans la famille des Papavéracées, *Glaucium corniculatum* (L.) Curt. se rencontre fréquemment. Les Crucifères sont abondantes : *Sisymbrium*, *Psychine*, *Savignya*, *Zilla*, *Eruca*, *Diploaxis*, *Erucastrum*, *Rapistrum*, *Muricaria*, *Capsella*, *Alyssum*, *Farsetia*, *Matthiola*, *Conringia*, *Moricandia*; la plupart sont bien acceptées par le bétail et constituent une ressource précieuse pour les troupeaux de moutons et de chèvres.

La famille des Légumineuses fournit des espèces intéressantes, notamment les Trigonelles (*Trigonella anguina* Delile, *Trigonella polycerata* L. var. *pinnatifida* (Cav.) Willk.), les Luzernes (*Medicago laciniata* (L.) Miller, *Medicago hispida* Gaertn., *Medicago orbicularis* (L.) Bart.), l'*Anthyllis tetraphylla* L., de nombreuses espèces d'*Astragalus* et de *Scorpiurus*.

Parmi les Plantaginacées, les Plantains (*Plantago albicans* L., *Plantago ciliata* Desf.) et les mauves parmi les Malvacées (*Malva aegyptiaca* L., *Malva parviflora* Lank) sont des plantes précieuses pour l'alimentation des moutons, elles sont abondantes surtout dans les pacages du Sud.

B — L'artemisaie de Chih

L'Artemisaie est pauvre en espèces, outre l'Armoise Herbe-blanc (*Artemisia Herba-alba* Asso) on trouve le *Lygeum spartum* L., localisé surtout dans les dépressions et les régions les plus imperméables; l'Harmel (*Peganum Harmala* L.) et diverses plantes fourragères épineuses (*Atractylis humilis* L., *Echinops*, *Lau-naea*). L'Armoise est considérée au Maroc oriental comme une ressource infiniment précieuse pour l'élevage du mouton.

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M. GUINOCHET (Alger)

Intérêt des notions d'association végétale, alliance et ordre pour la découverte et la définition des races écologiques

La notion de race écologique ou écotype fait intervenir deux concepts abstraits, celui d'unité systématique et celui de milieu. Pour un individu, ou, par extension, pour une population, le milieu où ils vivent est la résultante des effets combinés de tout ce qui leur est extérieur, c'est-à-dire de la totalité des facteurs physiques auxquels ils sont soumis et des êtres vivants qui les entourent. Etant donnée cette nature à la fois abstraite et synthétique de la notion de milieu, la définition des milieux naturels exige une méthode rendant compte de la totalité de l'information dont on dispose et excluant, en même temps, toute subjectivité: elle ne peut donc être que statistique. Il est aisé de démontrer qu'actuellement seules les unités phytosociologiques correctement utilisées répondent à ces exigences. Leur distinction repose, en effet, sur l'établissement de groupements floristiques statistiquement homogènes et sur l'évaluation, également statistique, du degré de liaison des diverses espèces à ces groupements. La méthode postule évidemment, que la composition floristique est le reflet exact du milieu: cette convention initiale est largement justifiée par l'expérience et par sa fécondité.

Il serait donc souhaitable que chaque fois qu'une race écologique est décrite, le milieu auquel elle est liée soit défini suivant ces principes, ce qui rendrait comparables, donc coordonnables, les résultats des divers chercheurs.

En outre, on voit que par sa nature même, la phytosociologie représente un excellent moyen, sinon le seul, de détection méthodique des espèces, ou unités subordonnées, chevauchant avec une certaine régularité —

d'ailleurs chiffrable — sur plusieurs types de milieux: il ne reste plus qu'à déterminer, par tous les moyens d'investigation qui nous sont offerts par la Science moderne si la forme systématique en cause a une large amplitude écologique ou est constituée d'un ensemble de races écologiques, ce qui est le plus souvent le cas. Voici quelques exemples d'espèces chez lesquelles on a plus ou moins récemment découvert et défini des écotypes grâce à la phytosociologie zuricho-montpellieraine: *Poa cenisia* All. (BRAUN-BLANQUET, J., Comm. S. I. G. M. A. n°2, 1929; n° 87, 1945); *Carex curvula* All. (GILOMEN, H., Ber. ü. d. Geobot. Forschungsinstitut Rübel i. Zürich f. d. Jahr 1937); *Cardamine pratensis* L. (GUINOCHET, M., C. R. Acad. Sc. Paris 222, 1946); *Deschampsia caespitosa* P. B. chez lequel on vient de découvrir une forme à $2n = ca. 42$ liée, sur le deuxième plateau du Jura, au *Calluneto-Genistetum* acidophile (M. GUINOCHET, résultats inédits); enfin, chez *Molinia coerulea* Moench on a mis en évidence des corrélations mathématiquement valables entre la localisation sociologiques d'une part et diverses données biométriques et physiologiques d'autre part, ce qui a conduit à modifier l'exposé classique des formes de cette espèce, tel qu'il avait été établi par ASCHERSON et GRAEBNER (GUINOCHET M. et LEMÉE, G., Rev. gén. de Bot., 1950, à paraître).

JEAN-PAUL HARROY (Bruxelles)

La nouvelle signification de la protection de la nature

L'Homme moderne qui, dès son enfance, se voit par sa famille et par ses maîtres, initié sans grandes peines aux fruits de millénaires d'empirisme, oublie volontiers que son ancêtre du Paléolithique, bien que doté de l'intelligence qui allait assurer à son espèce la maîtrise de la Terre, menait encore une existence pleine d'aléas et d'insécurité au sein de l'oppressante Nature qui l'environnait.

La chasse à laquelle se livraient les premiers hommes a longtemps ressemblé à celle que pratiquaient autour d'eux les carnassiers contre

qui ils avaient à se défendre. La cueillette des produits végétaux sauvages complétait pratiquement toutes leurs ressources alimentaires.

Bientôt, vers l'aube du Néolithique, grâce aux facultés de mémoire et d'invention qui lui sont spécifiques, l'Homme s'est imaginé de maintenir artificiellement à sa portée des groupes d'animaux ou de plantes reconnus par lui comme susceptibles de fournir des produits utiles à son économie. L'élevage et l'agriculture étaient nés, première forme d'une domestication des espèces ou des forces naturelles, que son ingéniosité croissante n'allait cesser de perfectionner et de généraliser au fil des temps.

L'empirisme, dont les tâtonnements dirigés portaient en germe l'investigation scientifique, a progressivement conduit à l'amélioration des espèces domestiquées, tandis que de nouveaux outils, de nouvelles armes de chasse ou de pêche, de nouvelles techniques culturelles étaient inventés qui venaient sans cesse renforcer la position de l'Homme à l'égard des groupements naturels dont il a de tous temps retiré et dont il retire encore aujourd'hui l'essentiel de ses moyens de subsistance.

Ces victoires de l'Homme sur la Nature se sont par endroits multipliées au point de modifier profondément les positions relatives de deux antagonistes. À l'origine, les occupations humaines constituaient des flots au sein d'associations naturelles vierges, souvent exubérantes sinon hostiles, lesquelles n'attendaient que l'occasion de reprendre pleine possession de chaque flot, sitôt que ses occupants humains l'abandonnaient. Avec le temps, toutefois, ces flots se sont multipliés, soudés les uns aux autres, étendus au point que la situation en fut inversée. C'est l'occupation humaine qui devenait la règle générale, tandis que l'association naturelle était ramenée au stade d'flot et prenait figure d'exception. L'Europe occidentale moderne, où l'influence anthropique s'est exercée sur la totalité du territoire, constitue, entre autres, un cas extrême de cette évolution.

Le XIX^e siècle et la première moitié du XX^e siècle ont démesurément accéléré ces occupations de l'Homme au détriment de son environ-

nement naturel, les possibilités d'application de l'empirisme utilitaire qui n'a cessé de présider à ces mises en valeur s'étant considérablement accrues par suite des inventions techniques.

Il n'est pas superflu de s'arrêter un instant à caractériser quelques-unes des multiples formes de troubles que l'action humaine apporte de nos jours — et quelques-unes depuis fort peu d'années — au sein des associations naturelles de la Planète. Cette énumération vise un triple but: évoquer la multiplicité de ces perturbations; montrer combien certaines de celles-ci ont accentué leur incidence depuis les dernières décades; et souligner enfin combien souvent ces interventions comportent encore des conséquences imprévues, anthropocentriquement fâcheuses. Ici reparassent les dangers de la généralisation excessive de l'empirisme utilitaire, sans un essai de synthèse préalable. Les conséquences fâcheuses de ces initiatives, leurs auteurs n'avaient pas cherché à les prévoir... Parfois même, ils ne les percevaient pas ou alors ils en rejettent la responsabilité sur d'autres causes.

Exactement comme son ancêtre des cavernes, mais avec des moyens d'action combien plus puissants, l'Homme moderne retire des associations naturelles, par chasse, pêche ou cueillette, les organismes végétaux ou animaux sauvages qu'il convoite afin d'en incorporer certaines parties dans ses produits de consommation. Si ces prélèvements gardaient la proportion d'une perception d'intérêt, l'opération pourrait durer indéfiniment, les troupeaux et les peuplements végétaux se reconstituant à mesure des abâtages ou des récoltes. Il en fut ainsi aussi longtemps que l'imperfection des armes et des outils et que l'organisation économique des groupements humains ont empêché qu'il en fût autrement. Mais de nos jours, l'équilibre est rompu. Seule, la sagesse de l'Homme pourrait éviter que la perception d'intérêt devienne une consommation de capital. Cette sagesse, que les défenseurs des intérêts de la collectivité ont souvent prêchée et quelquefois fait triompher, le consommateur individuel ne l'a pas pratiquée. Et l'on sait à quel prix. Les millions de Bisons

d'Amérique, base alimentaire de peuples entiers, ont été exterminés pratiquement jusqu'au dernier. Plusieurs dizaines d'espèces de Mammifères et d'Oiseaux ont disparu au cours des trois derniers siècles de la surface de la Terre. Beaucoup sont actuellement menacés d'extinction. Le rendement de la pêche en mer et en eau douce a, par endroits, dangereusement diminué, consécutivement à la mise en oeuvre de techniques puissantes trop généreusement utilisées. Les espèces végétales n'ont pas été épargnées. Le *Raphia vinifera* a pratiquement disparu de Madagascar par suite des récoltes excessives dont il a été l'objet vers la fin du siècle dernier. Des communautés de plantes sont devenues rares au point d'être menacées de disparition et de nécessiter des mesures de protection sévères. On a cité sous ce rapport les flots survivants de forêts primitives au Peliliu, dans les îles du Palau (*Capparis carolinensis*), la forêt xérophile de l'île de Lanai aux îles Hawaii (plantes endémiques relictuelles), les îles Desventuradas (flore presque entièrement endémique), les hautes crêtes de l'île Sainte Héline, les forêts existant encore dans l'île de la Guadeloupe au Mexique, l'habitat du *Rafflesia Arnoldi* en Indonésie, la forêt relique du Mont Gouda dans la Côte française des Somalis.

Opération inverse de la précédente, l'Homme a fréquemment introduit dans certaines associations naturelles des espèces, végétales ou animales, qui leur étaient primitivement étrangères. Beaucoup de ces introductions furent involontaires, fruits soit de l'ignorance, soit de la négligence. Les effets n'en sont pas moins innombrables, souvent fâcheux, souvent aussi très mal connus. Des espèces végétales ont été importées accidentellement d'un continent dans un autre et ont réussi à y occuper des millions d'hectares, tels l'*Imperata cylindrica* en Afrique, pour le plus grand dommage de la flore autochtone mal armée pour lutter contre cet envahisseur. Le crabe chinois, crustacé de grande taille qui constitue une menace pour le poisson d'eau douce dont il raréfie la nourriture et pour l'Homme dont il transporte un vecteur de maladie, a progressivement, accroché aux

carènes des navires, débordé de son habitat originaire, la Chine de l'Est, pour envahir les fleuves d'Europe occidentale où il occasionne aujourd'hui de sérieux dommages. La petite faune endémique de nombreuses îles des archipels d'Océanie a été décimée par la pullulation des rats, passagers des cales des vaisseaux au long cours qui y abordèrent. L'avion eut, d'autre part, le funeste privilège d'introduire involontairement au Brésil des moustiques infectés de malaria, avec les conséquences que l'on sait.

À côté de ces introductions involontaires, il en est bien d'autres qui, pour avoir été préméditées, n'en furent pas plus heureuses. Parmi ces opérations systématiques, il en est qui échouent, d'autres qui réussissent trop bien. Les premières, qui correspondant à l'éventualité où les associations autochtones parviennent à éliminer les espèces intruses, constituent simplement un déficit économique pour leurs promoteurs. Les autres, par contre, peuvent parfois tourner à la catastrophe. N'en citons qu'un exemple typique: la Lapin d'Australie, présent à toutes les mémoires. La pisciculture, l'agriculture, l'entomologie appliquée, pourraient en fournir bien d'autres. En matière de phytosociologie, les recherches de A. THELLUNG, de H. PERRIER DE LA BATHIE et de l'un des plus ardents et des plus compétents défenseurs de la flore d'Afrique, AUGUSTE CHEVALIER, ont jeté récemment de nouvelles lumières sur le processus compliqué de la propagation dans divers pays d'espèces envahissantes qui prennent progressivement la place des autochtones.

Troisième et importante intervention de l'Homme parmi les associations naturelles, la plus lourde, de loin, en conséquences diverses, est celle qui a pour objet de substituer à une formation ou à un groupement une autre formation ou un autre groupement estimé plus utile à l'économie humaine. C'est principalement l'opération du défrichement préliminaire à la mise en culture ou à l'ouverture au pacage. Sur des millions d'hectares, les forêts de la Terre, déjà si durement atteintes par les exigences de l'approvisionnement en bois du monde moderne, ont été, au cours de ces dernières

décades, rasées pour faire place à des cultures vivrières et industrielles. Les arbres et arbustes des savanes, les graminées des steppes et des brousses ont subi le même sort pour des motifs identiques ou pour permettre l'extension des élevages. En zone tempérée, où l'insolation et les précipitations sont également modestes, cette ablation du couvert végétal naturel ne comporte que de minimes inconvénients pour le sol ainsi dénudé. Mais il en va tout autrement entre les Tropiques — où pourtant les défrichements furent considérables depuis un demi-siècle — et où la dégradation pédologique et l'érosion ont tôt fait de marquer irrémédiablement un terrain superficiel privé, fut-ce pendant quelques semaines seulement de l'écran végétal qui le préserve habituellement contre les deux grands agents locaux de décomposition de la matière humique: les hautes températures et l'averse tropicale. Le développement récent de la technique de l'abatage, du dessouchage et du labour, dont l'entreprise britannique du «Ground Nut Scheme» au Tanganyika Territory, vient de démontrer simultanément la remarquable puissance et les multiples dangers, permet une extension sans cesse croissante de ces défrichements, extension que justifie, par ailleurs, un index démographique chaque année en progrès puisque le rythme d'accroissement de la population mondiale se situe actuellement aux alentours de deux cent millions d'unités tous les dix ans.

Des organismes divers, grands et petits, animaux et végétaux, entrent en compétition, dans ces nouvelles exploitations agricoles, soit avec le consommateur humain, soit avec les espèces dont celui-ci s'ingénie à favoriser la croissance et la multiplication. Ici des animaux sauvages dont l'habitat ancestral s'est vu récemment mué en champs cultivés, reviennent dans leur territoire natal, par habitude d'abord, mais encore parce qu'ils sont, eux aussi friands de ces tubercules ou de ces graines que l'Homme sème en rangs si agréablement serrés. Défense anthropocentriquement bien compréhensible, le «Game Control» a rendu un arrêt de mort définitif, sur des milliers de kilomètres carrés —

et principalement entre les Tropiques, une fois encore — contre des sangliers, des éléphants ou des zèbres coupables de trop apprécier les pommes de terre, le maïs ou le manioc. Ailleurs, le gibier sauvage a été accusé par le vétérinaire — autre nouveau venu au verdict sans appel, dont l'apparition dans d'innombrables territoires du Monde n'est pas antérieure au début du XXe siècle — d'être le réservoir à virus dont émanent tous les maux dont souffre le bétail domestique. Cet anathème a déjà été fatal à la grande faune sauvage du Nyasaland, de la Rhodésie du Nord, de certaines provinces de l'Uganda et du Kenya, dont l'extermination systématique, par la troupe, voire à l'aide d'armes automatiques, a été décrétée sous le signe du «rinderpest control» ou du «tse-tse control». Ailleurs, comme au Zoulouland, toujours sous le signe de la lutte contre les glossines, c'est la végétation qui a été rasée sur de grandes étendues, afin de détruire les gîtes des mouches, précisément à proximité de ces cours d'eau où le rôle protecteur des arbres et des arbustes est si important pour faire échec à l'érosion. Se greffant sur cet aspect de la question, songeons encore aux mesures prises un peu partout en région tropicale pour éliminer par drainage une humidité désagréablement propice à la prolifération de certains diptères piqueurs, mais qui, d'un autre côté, était peut-être un peu trop précise en ces zones habituellement sèches pour justifier qu'on l'envoie ainsi, par le plus court chemin, vers la mer, sous couleur d'assainir le pays ou d'y établir de nouvelles terres de cultures.

Une remarque générale, valant pour tout ce qui précède et tout ce qui suivra, peut s'énoncer avec propos immédiatement après cette dernière évocation: c'est le caractère inextricable des interactions en présence, qui complique pour le responsable de la manœuvre à choisir, la distinction entre l'utile et le dangereux, l'opportun et le nuisible. Telle mesure préconisée par le médecin sera réprouvée par l'agronome; et l'éleveur défendra parfois un programme que l'hygiéniste combattra avec énergie. Complication encore accrue singulièrement par la pauvreté des données biologiques dont dispose le

naturaliste consulté quant à savoir quelle espèce il y a véritablement lieu de considérer comme nuisible. Ennemi des basses-cours, le léopard a vu sa tête mise à prix peu partout en Afrique. Sa quasi-disparition dans certaines régions, suite à la chasse qui lui fut faite, a permis à ses anciennes victimes, les Babouins et les Cochons sauvages, de pulluler au point de commettre au détriment de l'Homme bien plus de dégâts que n'en commettait jadis le fauve tant exécré. Dans plusieurs territoires de l'Est Africain, le léopard vient de passer d'un seul bond de la catégorie des animaux nuisibles dans celle des mammifères protégés. De même au Congo Belge, l'accord est loin de se faire sur l'identité de celui des trois suidés sauvages, le Phacochère, le Potamochère ou l'Hylochère, qui mériteraient réellement une protection et de celui qui devrait, au contraire, figurer au tableau des animaux réputés nuisibles...

Le même brouillard d'ignorance environne encore l'usage, qui se généralise pourtant à un rythme inquiétant, de ces armes chimiques, mises au point tout récemment, et qui détruisent rapidement quelques espèces entomologiques jugées indésirables, au prix de l'extermination concomitante de très nombreuses autres associations au sujet desquelles beaucoup trop peu d'informations sont encore réunies. Une abondante littérature s'élabore actuellement sur les dangers de la généralisation trop hâtive du recours massif aux puissants insecticides modernes ou encore aux fongicides, aux herbicides et aux phytohormones. Mais l'usage se répand bien plus rapidement que ne peuvent se concevoir les précautions susceptibles d'en éviter les corollaires fâcheux. La protection des vergers belges contre certains parasites a déjà, par endroits, été fatale à l'apiculture. Et une désinsectisation trop parfaite des champs de tournesol de la Overseas Food Corporation, à Kongwa — Tanganyika Territory — en a par endroits compromis la fécondation des fleurs et le succès de la culture.

Une autre catégorie d'entreprises de l'Homme moderne visant à améliorer les chances de réussites de ses prélèvements parmi les ressource

ces naturelles correspond à ce que, notamment sous l'égide de l'Unesco, il est désormais admis de dénommer la lutte biologique. La tactique adoptée vise à favoriser l'introduction ou la prolifération d'organismes antagonistes de ceux estimés nuisibles aux entreprises poursuivies. En ordre principal, il est fait appel à des parasites ou à des prédateurs des insectes phytophages. Cette branche de l'entomologie appliquée se développe avec rapidité et l'on peut lire déjà des études sur des questions comme « les possibilités de l'Afrique Noire dans l'approvisionnement international en entomophages ». Mais l'on devine aussi les surprises que peuvent réserver à ceux qui osent s'y aventurer des domaines aussi riches en embûches de toutes sortes. Une fois de plus, l'image de l'apprenti sorcier se présente à l'esprit. Seule une réelle maîtrise des multiples aspects du complexe biologique mis en mouvement par l'apport artificiel d'un nouveau facteur, peut éviter à l'auteur de cet apport les aléas d'une aventure. Et cette maîtrise du sujet, seules peuvent y conduire des recherches scientifiques menées conjointement par des écologistes travaillant en équipes.

La Conférence Technique Internationale pour la Protection de la Nature qui s'est tenue au mois d'août dernier à Lake Success a abouti à des conclusions analogues. Elle a souligné les dévastations qui, partout dans le monde, marquent le développement trop brutal de l'économie moderne, que ce soit par des appauvrissements pédologiques, de l'érosion hydrologique ou éolienne, des destructions de forêts ou des ruptures d'équilibre de toutes natures dans les biotopes mis en valeur. Elle a, en une série de vœux, formulé l'espoir de voir se développer sous toutes ses formes l'étude écologique et, notamment, celle de l'écologie humaine. Le Conseil Economique et Social des Nations Unies envisage la création prochaine d'un Institut International des Sciences de l'Homme, dont une part importante de l'activité serait consacrée à cette discipline particulière.

Un peu de science éloigne de Dieu. Beaucoup de science en rapproche. Il en va de même de

nos rapports avec la Nature. Les premières atteintes portées aux associations naturelles par notre économie moderne, encore pleine d'une enfantine fierté pour sa technique toute neuve, ont été autant d'imprudences commises en toute et paisible inconscience.

Mais la Science, en progressant, sape notre sérénité et nous révèle chaque jour plus pleinement le caractère téméraire du jeu dangereux que nous avons entrepris de jouer. A la phase de confiance aveugle en la toute puissance des armes dont nous disposons pour asservir à nos volontés les complexes naturels commence à succéder une ère de doute et d'inquiétude. Nous voici à l'heure, qui finit toujours par sonner, où l'excessif optimisme fait place à un sévère retour sur soi-même et où un nouvel aspect des choses, jusqu'ici imperceptible ou volontairement négligé, vient occuper le devant de la scène. Le sort matériel de nombreuses collectivités humaines, malgré les progrès techniques de ces dernières décades, semble menacé par suite d'une approche insuffisamment prudente du problème de l'exploitation rationnelle des ressources naturelles. Le moment est venu d'en prendre pleine connaissance, et d'agir en conséquence.

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L'activité naissante de l'Union Internationale pour la Protection de la Nature peut être interprétée comme un indice encourageant de ce que l'humanité prend conscience de ses nouvelles responsabilités.

Les jours du pur empirisme utilitaire apparaissent désormais comme comptés. L'Homme s'est jusqu'ici ingénié à «arracher» à la Nature ses richesses sans s'inquiéter des répercussions de ses prélèvements sur la santé de sa mère nourricière. Et de même qu'une transfusion de sang ne peut se poursuivre jusqu'à épuisement total du donneur, de même l'opération en cours d'exploitation des ressources naturelles frôle, si elle ne l'a pas dépassé déjà, le point critique.

Le doute, l'inquiétude pénètrent progressivement dans les esprits. Mais l'espoir reste permis. Car l'étude désintéressée et complète de tous les aspects de cette évolution que l'Homme

moderne provoque et accélère, ouvre la voie vers les synthèses d'où sortira la solution. Et c'est dans cette voie qu'ambitionne de s'engager l'Union Internationale pour la Protection de la Nature.

C'est parce que des groupes d'hommes de divers pays, parmi lesquels il y a lieu de citer au 1^{er} rang l'Unesco et la Ligue Suisse pour la Protection de la Nature, se sont pleinement pénétrés de cette vérité, que le 5 octobre 1948 a été constituée, à Fontainebleau, l'Union Internationale pour la Protection de la Nature. L'acte constitutif de cette Union porte la signature des délégués de 18 Gouvernements, de 7 organisations internationales et de 107 organisations nationales s'occupant de Protection de la Nature. Au total 33 pays étaient représentés à la Conférence.

Le préambule de la constitution de l'UIPN est significatif. Il définit la «Protection de la Nature» dans son sens le plus moderne, juxtaposant heureusement la sauvegarde du monde vivant, milieu naturel de l'Homme et facteur primordial de toute civilisation, avec la défense des beautés naturelles, éternelles, sources d'inspiration de la vie spirituelle.

Désormais, l'heure est dépassée où l'idée de conservation se concentrait sur la promulgation de réglementations et sur la création de réserves naturelles et de parcs nationaux visant à sauvegarder des associations ou des espèces pour de seuls motifs esthétiques ou scientifiques.

A peine constituée, l'UIPN bénéficiera de l'aubaine inespérée d'être chargée de l'organisation scientifique de la Conférence Technique Internationale pour la Protection de la Nature que l'Unesco convoquait à Lake Success — conformément aux recommandations de son Assemblée Générale — pour le mois d'août 1949.

Le Conseil Exécutif de l'Union, à qui incombait la tâche délicate d'élaborer l'Ordre du Jour de ces assises internationales a pris le risque de rompre délibérément avec les normes classiques qui voulaient qu'à une réunion de ce genre, une place d'honneur fût faite à la technique juridique de la conservation et aux problèmes que pose la gestion des aires réservées.

Et c'est ainsi qu'au cours des treize séances de la Conférence l'accent fut mis principalement sur le problème de l'Education des enfants et des adultes dans le domaine de la conservation, sur le rôle prééminent que l'étude de l'Ecologie doit désormais jouer dans la protection et la sage gestion des ressources naturelles renouvelables de la Terre. Etendues à tous les règnes de la Nature, les préoccupations des participants n'ont pas négligé l'aspect botanique des problèmes posés et parmi les rapports déposés — dont le texte vient d'être publié en annexe aux Procès-Verbaux de la Conférence¹ — nombre d'entre eux concernent spécialement les perturbations que l'Economie moderne provoque au sein des associations végétales.

T. HOSOKAWA (Fukuoka)

On the Nomenclature of Aerosynusiae

DU RIETZ² systematized the units of plant communities, and proposed the system of corresponding units of phytocoenoses and of synusiae, or separate strata of biocoenoses, shown in Table 1..

Table 1

A comparative table of the units of synusiae and phytocoenoses.

Synusiae	Phytocoenoses
Panformion	Panformation
Formion	Formation
Subformion	Subformation
Federion	Federation
Associon	Association
Consocion	Consociation
Socion	Sociation

¹ Ceux que ces textes intéressent pourront éventuellement en obtenir un exemplaire de l'Unesco, en adressant leur demande au Secrétariat de l'UIPN, 42 rue Montoyer à Bruxelles.

Those who are interested in having this text can obtain a copy through the kindness of Unesco by writing to the Secretariat of the UIPN, 42 rue Montoyer, Brussels.

² DU RIETZ, G. E.: Classification and Nomenclature of Vegetation, Sv. Bot. Tidkr. XXIV. (1930) pp. 489—503, Tab. 1—3.

Table 2

A comparative table showing the units of synusiae and aerosynusiae.

Synusiae	Aerosynusiae
Panformion	Aeropanformion
Formion	Aeroformion
Subformion	Aerosubformion
Federion	Aerofederion
Associon	Aeroassocion
Consocion	Aeroconsocion
Socion	Aerosocion

This idea was of great help to plant sociological research. Being developed in temperate Europe, the system may be more or less modified for the study of vegetation in the tropical zone.

The author treats the synusiae of epiphyte societies as separated from those of terrestrial plants. He has proposed the new term of aerosynusia and a system of aerosynusiae, corresponding to DU RIETZ's system of synusiae. (Table 2.)

A research method of aerosynusiae. Set quadrats according to the research method of the terrestrial plants in forests. Then try to determine the presence degree and the grade of sociability of the vascular epiphytes on trees in every quadrat, and at the same time try to investigate the vertical distribution of epiphyte species in forests according to each habitat respectively. That is to say, when the habitats of vascular epiphytes on trees are classified into four, viz. crowns, crown-bases, trunks and trunk-bases, we can determine the grade of sociability of epiphytes in accordance with each habitat, including investigation of the vertical distribution of epiphyte species according to each habitat. As a result of such investigations, various strata of aerosynusia are recognized. In the tropical rain forests in Micronesia, the writer usually distinguished three aerosynusiae, viz. with sunny arid, intermediate and shady humid environment, but in the mangrove forests only one aerosynusia with sunny arid environment,

Table 3

An example of determination of aeroconsociation from the data of the Q_1 — Q_{21} in the *Campnosperma brevipetiolata* consociation (30—340 m above sea level) in the Ponape island. The table shows the presence degree and the grade of sociability of the epiphytes, from which some aeroconsociations, viz. *Dendrobium carolinense* aeroconsociation (sunny arid society), *Neottopteris nidus-Procris ponapensis* aeroconsociation (intermediate society) and *Crepidopteris humilis* aeroconsociation (shady humid society) are recognized.

Life-form ¹	Epiphyte species	Grade of sociability				Presence degree
		Crowns	Crown-bases	Trunks	Trunk-bases	
F	<i>Ophioderma pendulum</i> Presl			+	+	1
O	<i>Cephalomanes boryanum</i> v. d. Bosch				+	1
Fi	<i>Crepidomanes bipunctatum</i> Copel.				+	+
Fi	<i>Crepidopteris humilis</i> Copel.				+++	3
Fi	<i>Gonocormus minutus</i> v. d. Bosch			+	+	1
Fi	<i>Mecodium polyanthos</i> Copel.			+	+	+
Fi	<i>Microgonium craspedoneurum</i> Copel.				+	1
Fi	<i>Microgonium omphalodes</i> Viellard			+		2
F	<i>Antrophyum callifolium</i> Bl.		++	+		2
Rr	<i>Davallia embolostegia</i> Copel.	+	+			1
Rr	<i>Davallia solida</i> Sw.	++	+			2
Rr	<i>Goniophlebium ponapense</i> Copel.		+	+		1
Rr	<i>Humata trukensis</i> H. Ito	+	+			1
Rr	<i>Lepisorus accedens</i> Hosokawa	++	+			2
O	<i>Lindsaya ambigens</i> Ces.				+	1
F	<i>Neottopteris nidus</i> J. Sm.	+	+	++	+	5
Rr	<i>Nephrolepis hirsutula</i> Presl	+	++	+		2
Rr	<i>Phymatodes scolopendria</i> Ching	+	+	+		1
F	<i>Tarachia adiantoides</i> Nakai		+	+		2
F	<i>Tarachia cuneata</i> Presl		+	+		+
F	<i>Tarachia laserpitiifolia</i> Presl		+	+		2
Rd	<i>Vaginularia paradoxa</i> Mett.			+		2
Rd	<i>Vittaria angustata</i> v. A. v. Rosenburgh			+		1
Rd	<i>Vittaria elongata</i> Sw.		+	+		1
F	<i>Schizaea ponapensis</i> Hosokawa			+		1
C	<i>Urostachys phlegmaria</i> Hert.	+	+			1
C	<i>Urostachys squarrosus</i> Hert.	+	+			+
O	<i>Selaginella Kanehirae</i> Alston				+	+
Eph	<i>Freycinetia ponapensis</i> Martelli				+	+
Eph	<i>Bentinckioopsis ponapensis</i> Becc.				+	+
C	<i>Aglossorhyncha</i> vel <i>Glomera</i> sp.	+				+

¹ Refer to T. Hosokawa's "Studies on the life-form of vascular epiphytes and the spectrum of their life-forms", in Journ. Jap. Bot. XXIV. (1949) pp. 41—45, in which the modified system of life-forms are described; e.g. *F⁴* (= Epiphyte unistrato-cellularis) is a life-form of vascular epiphytes, which is characterized by the mesophylls in leaves being composed of 1 layer of cells, as in such epiphytes

as filmy ferns. The other life-forms, such as *D*, *SV*, *Mc*, *Rr*, *Rd*, *C*, *F*, *Rt*, *Se*, *He*, *O*, and *Eph* were proposed by the author, who published them already in an article on "Studies on the life-forms of vascular epiphytes and the epiphyte flora of Ponape, Micronesia", in Trans. Nat. Hist. Soc. Formos. XXXIII. (1943) nos. 234—236.

Life-form	Epiphyte species	Grade of sociability				Presence degree
		Crowns	Crown-bases	Trunks	Trunk-bases	
Rd	<i>Bulbophyllum ponapense</i> Schltr.	+				+
C	<i>Dendrobium carolinense</i> Schltr.	++	+	+		3
C	<i>Dendrobium flavicollis</i> Schltr.	+	+	+		1
C	<i>Dendrobium ponapense</i> Schltr.	+	+			2
C(Se)	<i>Dendrobium violaceo-miniatum</i> Schltr.	+	+	+		+
C(Se)	<i>Oberonia Hosokawae</i> Fukuyama	+				+
C	<i>Phreatia Pseudo-Thompsonii</i> Tuyama	+				+
C	<i>Phreatia Thompsonii</i> Ames	+				+
He	<i>Pseuderia micronesiaca</i> Schltr.		+	+		1
F	<i>Taeniophyllum petrophilum</i> Schltr.	+				+
Mc	<i>Thrizpermum arachnitiforme</i> Schltr.	+				+
Rr(Se)	<i>Peperomia brevifolia</i> C. DC.	+	+	+	+	1
Eph	<i>Piper ponapense</i> C. DC.				+	+
He	<i>Ficus carolinensis</i> Warb.		+			+
He	<i>Ficus tinctoria</i> Forst.		+			+
SV(Se)	<i>Procris ponapensis</i> H. Schroeter		+	++		5
He	<i>Fagraea sair</i> Gilg & Benedict		+			2
Eph	<i>Hoya Schneei</i> Schltr.				+	+
Total number of epiphyte species in each habitat		21	25	22	15	
Total number of epiphyte species in the <i>Campnosperma brevipedunculata</i> consociation		49				

Table 4

The spectrum showing percentage of life-forms of vascular epiphytes in the three aeroconsociations in the *Campnosperma brevipedunculata* consociation of Ponape. As *Se* is a life-form generalized with regard to succulency of all life-forms, it will be better to count it up independently and show it in percentage of the total species-number.

Aerousynusia	Habitat	Environmental character	Fi	D	SV	Mc	Rr	Rd	C	F	Rt	(Se)	He	O	Eph	Total number of species
<i>Dendrobium carolinense</i> aeroconsociation	Crowns and crown-bases	Sunny arid			3	3	25	6	31	19		(13)	13			32
<i>Neottopteris nidus</i> - <i>Procris ponapensis</i> aeroconsociation	Trunks	Intermediate	14		5		18	14	14	31		(14)	5			22
<i>Crepidopteris humilis</i> aeroconsociation	Trunk-bases	Shady humid	33				7			13		(7)		20	27	15

and in the scrubs on montane ridges two aerosynusia with sunny arid and intermediate environment. Investigating the Micronesian vegetation, the writer selected the epiphytes giving high values in presence degree and the grade of sociability on each habitat of trees as the representatives of aerosocios. The writer distinguishes the following three grades of sociability:

- + growing sparsely and in few individuals.
- + + growing in abundance.
- + + + growing very densely and very abundantly.

In each consociation, the epiphyte species giving high values of presence degree and grade of sociability from several quadrats are selected as the representatives of the aeroconsociation. The determination of the aeroassociation in the association is made with the same method.

Table 4 is derived here from Table 3. The author recognizes in the *Campnosperma brevipetiolata* consociation of Ponape that the *Dendrobium carolinense* aeroconsociation is characterized by the life-forms of *Rr*, *C*, and *He* as an aerosynusia including the aerosocios developed in crowns and crown-bases of trees, i.e. sunny arid environments, that the *Neottopteris nidus* - *Procris ponapensis* aeroconsociation is characterized by the life-forms of *F* and *Rd* as an aerosynusia including the aerosocios developed on trunks, i.e. intermediate environments, and that the *Crepidopteris humilis* aeroconsociation is characterized by the life-forms of *Fi*, *O*, and *Eph* as an aerosynusia including the aerosocios developed on trunkbases, i.e. shady humid environments.

Comments

G. E. DU RIETZ: As mentioned above on p. 664, the terms proposed by myself in 1930 for the lower units of synusia—consociation, association and federation—were abandoned already

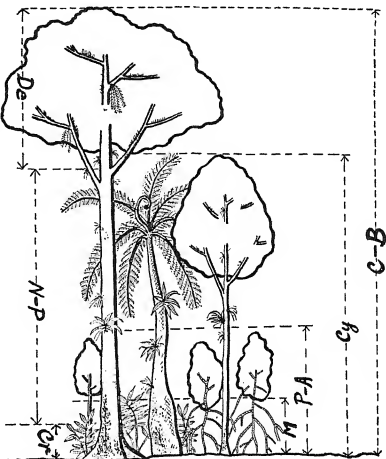


Fig. 1. Model of synusia and aerosynusia in the *Campnosperma brevipetiolata* - *Benthickiopsis ponapensis* association of Ponape. Abbreviation in the synusia: C-B = *Campnosperma brevipetiolata* - *Benthickiopsis ponapensis* association, Cy = *Oyathia nigricans* association, P-A = *Pandanus Cominsii* - *Aglia ponapensis* association and M = *Marattia Mertensiana* association. Abbreviation in the aerosynusia: De = *Dendrobium carolinense* association, N-P = *Neottopteris nidus* - *Procris ponapensis* association and Cr = *Crepidopteris humilis* association.

in 1935 by agreement between GAMS, LIPMAA and myself, and replaced by the terms society, union and federation (Sv. Bot. Tidskr., 30, 1936). These terms have since then been widely used in European, and partly also in American, phytosociology. In my concept of synusia, also epiphytic communities were included (Ibid., 39, 1945, pp. 147—150, where various epiphytic federations (or "förbund" in Swedish) and unions were described). In the terminology used by myself and many other European phytosociologists since 1935, Hosokawa's aerosocios should be called societies, and his aerosocios unions.

PHYTOPATHOLOGY, PHP

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SESSION 1

July 12th, 2—4 p. m., Attendance: 70 members

Chairman: E. C. STAKMAN, Recorder: K. BJÖRLING

SUBJECT:

Adaptation of Phytopathogens to Different Host Plants

HELENA DE BRUYN (Wageningen) *Adaptation of Phytophthora infestans to Various Potato Hybrids*

It has been proved (MILLS) that isolates of *Phytophthora infestans* from potatoes can adapt themselves to tomatoes by a number of passages, the pathogenicity for tomatoes increasing gradually. The problem of the existence of races of this parasite has therefore become doubtful. Wherever potato hybrids of *Solanum tuberosum* with another *Solanum* species have been cultivated new forms of *Phytophthora* have come into existence. It has never been established whether these new races in the different countries were identical. In Germany the S-race was found and could be recognized by its ability to attack the W-varieties of potatoes (hybrids), later distributed as the varieties Aquila, Erika, Frühnudel, Robusta. The generally occurring *Phytophthora* attacking all potato varieties of *Solanum tuberosum* was called the A-race. Just as MILLS had changed the potato *Phytophthora* into a tomato *Phytophthora*, it was possible by passage through the

different hosts to alter the A-race into an S-race. Both A- and S-race of potatoes could be changed into a tomato-race. In the last case, however, the S-race lost the ability to attack the W-varieties of potatoes. After treatment no difference could be observed between the originally unequal potato-races. Various isolates, all starting from a single zoospore and of different origin, were adapted to either the W-varieties of potatoes, to tomatoes or to various potato hybrids. It was proved that the original source of the isolate was of no importance. Those adapted by some passages to the tomatoes, to the W-varieties or some special hybrid, behaved according to their treatment. Their pathogenicity to special hybrids was alike if they had passed the same plants independent of their original source. It is thus impossible to maintain the proposed division into races of *Phytophthora infestans*. There may exist races but they must be distinguished from each other by other characters than have been used until now. The plasticity of the parasite being proved, the limits of this plasticity may be one of the characters taken into considera-

tion. It will, however, not be easy to settle the matter or to build up a good test series for exact pathogenicity grades.

Discussion

MARGARET KEAY: The Commonwealth Potato Collection, Cambridge, England, contains various wild and cultivated species of *Solanum* from Mexico and S. America. These provide a source for developing a panel of differential hosts for identifying physiologic races of *Phytophthora infestans*. It is hoped to select a panel of homozygous lines which reproduce freely by true seed.

HELENA DE BRUYN: I quite agree with the remarks of Miss KEAY. It should be favourable to have a good collection of *Solanum* species for testing the pathogenicity of the parasite.

K. O. MÜLLER: Die Auffassung, dass dem Entwicklungszustand der Wirtspflanze eine wesentliche Bedeutung für das parasitische Verhältnis zukommt, ist unbedingt beizupflichten. Auch können wir auf Grund von Untersuchungen, die in Berlin-Dahlem und neuerdings in Cambridge durchgeführt wurden, bestätigen, dass beim Parasiten "Mutationen," ganz vorsichtig ausgedrückt, sprunghafte Änderungen sowohl in morphologischer und entwicklungsphysiologischer wie in parasitologischer Hinsicht auftreten. Dass es sich bei unseren Versuchen lediglich um Entmischungen von Populationen des Parasiten handelte, ist ausgeschlossen, da Stämme benützt wurden, die aus einzelnen Zoosporen (einkernig) herangezogen waren. Doch konnten wir unter strengsten kontrollierten Bedingungen was die Virulenz des Pilzes anbelangt, bisher nur Minus-"Mutationen" ermitteln. Dass schliesst selbstverständlich nicht aus, dass auch Änderungen in entgegengesetzten, also im Sinne einer Virulenzsteigerung auftreten, zumal unter den "üblichen" Laborbedingungen und im Gewächshaus auch von uns Änderungen beobachtet wurden, die denen entsprechen, die von Fräulein DE BRUYN geschildert worden sind. Doch ging die Plastizität nicht so weit, dass dadurch, dass man

den Pilz auf nicht zusagenden Wirten zu leben zwingt, die Virulenz "beliebig" geändert werden könnte. Darüber hinaus fanden wir im Laufe einer Beobachtungszeit von 12 Jahren, dass solche "positiven" Änderungen immerhin recht selten sind. Diese relative Konstanz der von uns isolierten Linien des Parasiten gestattete uns auch (1944), an Hand eines eigens zu diesen Zweck gezüchteten Testsortimentes 31 verschiedene "biologische" Formen bzw. Rassen zu unterscheiden, wobei sowohl der Blatt- wie der Knollentest benutzt wurde.

Das Problem der Virulenzänderungen bei *Phytophthora infestans* dürfte nicht nur den Kartoffelzüchter — für ihn ist die „Anpassungsfähigkeit“ des Parasiten von geradezu entscheidender Bedeutung —, sondern auch den Genetiker und den Phytopathologen stärkstens angehen. Im Grunde handelt es sich um die Entscheidung der Frage, ob die Beobachtungen der Virulenzänderungen im Sinne einer neolamarckistischen Anpassungstheorie zu deuten sind, oder ob es sich hierbei um richtungslose, sprunghafte Änderungen im Sinne der modernen Mutationengenetik handelt. Letzterenfalls würde der resistente Wirt nur als Selektionsfilter wirken. Dieses Problem ist auch heute noch als ungeklärt zu bezeichnen. Nichts destoweniger neige ich noch wie vor dazu, die von MILLS, REDDICK, BLACK und um von de BRUYN beschriebenen Virulenzänderungen im Sinne der zweiten Alternative kausal zu erklären. Dies umso mehr, als sich auch in der Bakteriologie mehr und mehr die Tendenz durchsetzt, analoge Veränderungen bei Einzellkulturen von tierpathogenen Bakterien als Folge von Mutationen zu deuten. Das heisst aber, dass man an der Existenz verschiedener "biologischer" Rassen oder Formen (welche Bezeichnung wir wählen, ist m.E. von zunächst untergeordneter Bedeutung) auch bei *Phytophthora infestans* festzuhalten hätte.

H. ROSS: Nachdem bisher sämtliche Demisum-Hybriden im Verlauf von wenigen Jahren vom Pilz befallen wurden, wird es nötig sein, den Resistenztyp zu untersuchen, den die Wildarten *Solanum polyadenium*, einige Herkünfte

von *S. antipovicii* und andere *Longipedicellata*, sowie auch einige Herkünfte von *S. demissum* besitzen. Diese Arten sind nach 10-12-jähriger Kultur in unmittelbarer Nachbarschaft von Kultursorten nicht befallen worden. Es ist möglich, dass die *Phytophthora* mit ihren Varianten nicht imstande ist, den Resistenztyp dieser Wildarten zu überwinden. Es laufen im Institut in Voldagsen Versuche von Dr. SCHAPER, die hohe Resistenz dieser Wildarten züchterisch auszuwerten.

W. A. F. HAGBORG (Winnipeg, Man.)

Adaptation of Xanthomonas translucens to Different Host Plants

Several *formae speciales* occur in *Xanthomonas translucens* Hagb. They have many attributes in common, but differ in their adaptation to different hosts and parallel closely the type *formae speciales* of *Puccinia graminis* Pers. as described by Eriksson. *X. translucens* f. sp. *undulosa* (S. J. & R.) Hagb. and *X. translucens* f. sp. *cerealis* Hagb. occur commonly on *Triticum* and *Secale* respectively. In studies made on the prevalence of bacterial diseases of cereals, they were isolated from 120 different Canadian collections of diseased wheat and rye plants. Either *X. translucens* f. sp. *hordei* Hagb. or *X. translucens hordei-avenae* Hagb. were isolated from 32 field collections of diseased barley plants grown under conditions of natural infection. *X. translucens* f. sp. *undulosa* was recovered once from barley in a field plot, but only following inoculation with it.

Studies made thus far suggest a relatively high stability in the *formae speciales* of *X. translucens*. Two different isolates of each of f. sp. *undulosa*, f. sp. *cerealis* and f. sp. *hordei-avenae* were cultivated in parallel series through successive transfers, one series on nutrient agar and the others on the host plants. After every second transfer each culture was tested for pathogenicity on the four cereal hosts, wheat, oats, barley, and rye. No evidence of variation occurred throughout the test except that attributable to environmental influences and in

all instances the original *forma specialis* was recovered at the end of the test. Similarly no differences were detected in the pathogenic capabilities of cultures of monoclonal origin from the same *forma specialis* and in cultures grown on broth previously treated with sub-lethal doses of hydrogen peroxide. One culture originating in one of 44 single colonies that grew from cells surviving an X-irradiation of 20 000 roentgens, appeared to be somewhat changed in pathogenic capabilities. Further tests will be made in an attempt to establish whether or not this culture originated as a mutant induced by irradiation.

Although biological specialization is less well-known in the bacteria than in the fungi, it is a characteristic of bacterial phytopathogens as of fungal phytopathogens. The use of the designation "*forma specialis*" is an attempt to recognize the phylogenetic significance of biological specialization and at the same time provide a means of referring to biologically specialized groups. Probably future studies will show that many bacterial phytopathogens now known under species names ought to be classified as *formae speciales*. Revisions of classification in that direction may do much to reconcile the views of the plant pathologist with those of the bacteriologist-serologist.

G. M. ARMSTRONG and L. K. ARMSTRONG
(Clemson, S. C.)

A Comparison of the Host Relationships of the American, Indian, and Egyptian Cotton-Wilt Fusaria

Previously the U. S. cotton-wilt *Fusarium* was found to cause wilt of Burley tobacco and okra, and a slight wilt of *Cassia tora*. With Burley tobacco as a common host, the following biological races were found: (1) the race mentioned above did not cause wilt of sweet potato; (2) a race which caused wilt of Burley tobacco and sweet potato but not of flue-cured tobacco and cotton; (3) a race which caused wilt of sweet potato, Burley and flue-cured tobacco, but not of cotton; (4) a recently found

race which caused wilt of Burley and flue-cured tobacco, cotton, and Yelredo soybean, but not of sweet potato. The *Fusarium* of (4) is not the same as the soybean-cowpea-wilt *Fusarium* reported recently. A virulent wilt *Fusarium* of *Cassia* has been found which is different from the cotton-*Cassia* wilt (1) above. This fungus is weakly virulent on cotton but caused wilt of another host, alfalfa (Kansas Common). The common alfalfa-wilt *Fusarium*, however, does not cause wilt of *Cassia*. The cotton-wilt *Fusaria* from the U. S., India, and Egypt on varieties of *Gossypium hirsutum*, *G. arboreum*, *G. herbaceum*, and *G. barbadense* differentiate into three biological races. These results, however, are at variance with published results since there are varieties of the last three species above which are resistant to all three races of the fungus and some susceptible to all three. The Indian and Egyptian fungi did not cause wilt of eight *G. hirsutum* varieties. The inadequacies of existing systems of classification are indicated.

N. T. FLENTJE (London)

Specialization and Variation in Rhizoctonia Solani Kühn

The interaction of different isolates of *R. solani* with certain plants (e.g. lettuce, tomato, cabbage, etc.) ranges from high susceptibility shown by progressive damping off, to complete insensitivity. From a wide range of isolates one can sort out certain groups or strains of the fungus and label them as belonging to the "crucifer type", that is they actively cause damping off in crucifer seedlings and so on for other groups. The distinction however is not hard and fast, e.g. an isolate of the crucifer type can produce lesions on lettuce or tomato, these hosts however having the capacity to resist progressive invasion. Furthermore the resistance of a host may vary in its different parts; e.g. leaves

of lettuce are actively invaded by a crucifer strain which is unable to progress in the hypocotyl. Also the resistance of lettuce hypocotyl to progressive invasion by the crucifer strain breaks down if the plant is sufficiently etiolated.

Microscopic study of the behaviour of the fungus in the presence of a potential host has revealed interesting details of pre- and post-penetration effects.

Pre-penetration

When *R. solani* meets a host to which it is not pathogenic, the hyphae behave in the same way as when meeting a glass rod; they show no reaction but merely grow around the obstacle. Then there are intermediate conditions up to the other end when *R. Solani* meets a host in which it causes damping off. In this latter case the hyphae immediately respond to some stimulus, orientating themselves on the hypocotyl, adhering firmly to it, and forming a complex structure called an infection cushion.

In all cases examined, wherever attack took place there was a greater or less build up of external hyphae as a preliminary. However such a build up is not of itself a complete guarantee of successful invasion. Invasion took place but other factors determined whether it developed actively.

Post-penetration

The contrast here is between progressive and arrested invasion. The latter type was characterized by complete cessation of growth of invading hyphae, the death of invaded and contiguous host cells, and the development of a mustard brown or dark brown colour in these host cells. As far as could be determined the hyphae in these lesions were dead. This then is the hypersensitive reaction or something very like it. One would therefore suggest that a study of *R. solani* on a variety of hosts offers promise of a better understanding of this important reaction.

SESSION 2

Jointly with Section AGR: July 14th, 9 a. m. — noon, Attendance: 110 members

Chairman: W. H. BURKHOLDER, Records: K. BJÖRLING and E. ÅKERBERG

SUBJECT:

Immunity and Resistance Caused by Hypersensitivity Reactions

K. O. MÜLLER (Cambridge)

The Hypersensitivity Reaction of the Potato to Phytophthora Infestans from a Genetical and Phytopathological Point of View

The reactive resistance to *Phytophthora*, possessed by the 'W varieties', certain *Solanum demissum* forms and their hybrids with common European varieties is effected by hypersensitivity (MÜLLER, MEYER). As shown by MÜLLER (1928, 1930), LEHMANN (1941) and BLACK (1944–1949), the resistance is inherited in the Mendelian fashion; the number of genes involved here is relatively small and, so far as the present material suffices, we can draw the conclusion that these genes are dominant. On the other hand, there are rather numerous strains of the parasite which differ with their biological specialisation to the different host types. As SCHICK, MÜLLER, BLACK and HAIGH have found, this specialisation is multidirectional. Moreover, as BLACK made clear, the same gene might control resistance to different strains and different genes to the same strain.

In order to throw some light on the nature of the host-parasite relationship which is controlled by these genes, the author and his pupils investigated the morphological and physiological changes which the infected tissues of the different host genotypes undergo under the influence of the parasite. The main results of these investigations may be summarized as follows:

1) The phenotypical effect of the genes which control the sensitivity of the affected tissues is chiefly characterised by the velocity with which the infected cells react to the invading parasite.

2) There are different degrees of reaction-rate. Examining analogous organs of F_2 forms from crosses between resistant and susceptible genotypes, it becomes obvious that the greater the reaction-rate, the greater the resistance of the plants. We find the same if we compare the various tissues of the same genotype.

3) The reaction to the invading parasite ends in any case with the death of the infected cells. At least five phases in the complete course of the reaction can be distinguished; in the most susceptible genotypes and tissues this reaction is often not completed because the affected cells die before the last stages are reached.

4) The reacting cells release in dying a substance (or substances?) which exerts a fungistatical effect on the parasite 'phytoalexin'. After a certain period the fungistatical effect changes into a fungicidal one.

5) The immunological effect of this defense reaction is unspecific, i.e. the refractory behaviour of the plant to the different *Phytophthora* strains does not depend on the specificity of the final stage of the reaction, but on the *specific sensitivity* of a certain basic system which becomes efficient *after* having been affected by the parasite.

6) Such a system, probably an enzymatic one, is possessed not only by the so-called resistant species of the family *Solanaceae*, but also by rather numerous other families of the division *Angiospermae*.

7) The multidirectional specialisation of the different blight strains and the unspecificity of the defense reaction lead us to the conclusion that there are several 'partial sensitivities' (Partial-Sensitivitäten), each of them controlled by significant genes. On the other hand, we

may suggest that there are correspondingly different pathogenic 'activities' of the parasite. This conception is supported by results of breeding and pathological experiments.

Thus experimental results and theoretical considerations make obvious that the reactive *Phytophthora* resistance (or vice versa susceptibility) is not a quality, such as petal colour or leaf shape, but rather is a *functional* character which becomes operative only when direct contact has been established between host and parasite. Therefore, that which is significant for the 'hypersensitive' blight resisters is really not a gene or genes for blight resistance itself, but rather genes controlling a reaction *potential*, possessed not only by the genus *Solanum*, but also by other groups of the division *Angiospermae*.

As will be shown, this conception of the nature of the hypersensitivity to blight infections offers a theoretical explanation of the findings of BLACK and MÜLLER, concerning the inheritance of blight resistance, and of the mechanism of the biological specialisation of *Phytophthora infestans* to the different hosts.

A. J. OORT (Wageningen)

Hypersensitivity of Wheat to Loose Smut

One of the ways by which a plant may defend itself against biotrophic parasites is a reaction which may be ascribed to hypersensitivity. Parts of the host die as a consequence of infection and prevent spreading of the parasite, which is dying in its turn. Fungi belonging to different groups (*Archimycetes*, *Phycomycetes*, *Ascomycetes* and *Basidiomycetes*), higher plants (*Viscum*), biotrophic insects (*Rhynchota* like *Eriosoma* and *Phylloxera*), and probably biotrophic nematodes as well, may bring about this hypersensitivity reaction in some varieties of the host. Viruses, which are comparable to biotrophic parasites, also may cause such heavy reactions that they are localized and do not propagate.

During experiments on Loose Smut of Wheat (*Ustilago tritici*) a phenomenon was observed

which had to be ascribed to hypersensitivity. A detailed study of the plant-parasite relationships revealed the fact that two principles are working together in each plant as regards the reaction to the fungus. These two principles are working quite independently of one another.

I. The host is susceptible to a higher or lesser degree or it is resistant.

II. The host reacts either by hypersensitivity or is sensitive. In the last case sensitivity means that the host develops smutted ears quite normally. When infected seed of a variety which is hypersensitive to the parasite is sown in the greenhouse under favorable conditions the seedlings look quite ill and several of them die in the two to four leaf stage. Leaf blades and sheaths develop abnormally, they are short and curled and show chlorotic stripes. In a congenial (sensitive) host variety seedlings are quite normal in appearance and they cannot be distinguished from not infected ones.

The plants which do not die in the seedling stage, recover slowly. Symptoms do not occur in the higher leaves, healthy ears develop. Ears and stems, however, are generally smaller and shorter than normal. Observations indicate that recovery must be attributed to the development of healthy side shoots whereas the main shoot generally dies in the seedling stage. In the very exceptional case that the main shoot remains alive, the higher leaves are also distorted and sometimes a few smut stripes develop in the much dwarfed ears. The very heavy reaction of the plant has all the characteristics of a hypersensitivity reaction. In most cases the host perishes together with the parasite before the last has been able to produce spores. The plant reacts either by hypersensitivity or by sensitivity. Intermediate reactions are not met with.

The principle of susceptibility-resistance is present in plants which show smutted ears as well as in plants reacting with hypersensitivity. This means that this case is not in agreement with the idea brought forward by GÄUMANN in *Pflanzliche Infektionslehre*, as hypersensitivity is not the end stage of a series which

starts with resistance and goes on increasing susceptibility to a form of resistance which is called hypersensitivity.

R. BAUER (Voldagsen/Elze)

Immunität und Resistenz gegenüber

Sphaerotheca mors uvae (Schw.) Berk. bei Ribes

Der Erreger des amerikanischen Stachelbeermehltaues ist ein obligat biotropher Epidermisparasit. Bei künstlicher Infektion unter für den Parasiten optimalen Entwicklungsbedingungen (Gewächshaus) tritt bei den meisten Arten eine Verschiebung der Reaktionslage nach "anfällig" auf. Es entwickeln sich dabei artspezifische Befallsbilder. Unter den untersuchten Arten blieben nur zwei befallsfrei.

Zur Klärung der Ursachen der beobachteten Befallstypen (0 bis 4) wurde nach künstlicher Infektion die Entwicklung des Parasiten und das Verhalten der infizierten Organe mikroskopisch verfolgt. Art, Grösse, Zahl und Zustand der Haustorien und Hyphen einer Einsporkolonie ermöglichen in Verbindung mit dem Zustand und dem Verhalten der Wirtszelle eine qualitative und quantitative Erfassung des jeweils bestehenden Parasit-Wirtsverhältnisses.

Die durchgeführten Befallsanalysen zeigten, dass die geimpften Oidiosporen auf allen untersuchten *Ribes*-Arten "haften" durch Ausbildung eines Hafthaustoriums. Unterschiedlich ist nur ihr weiterer Entwicklungsgang. Dieser wird bestimmt durch die jeweilige Reaktionslage der infizierten annuellen Organe, die im Ablauf der Ontogenese eine dreifache Änderung erfährt:

Phase I: Widerstandsfähigkeit in embryonalen, sich teilenden Epidermien, Phase II: Anfälligkeit in auswachsenden, sich streckenden Epidermien, Phase III: Widerstandsfähigkeit in ausgewachsenen, "reifen" Epidermien. Die Jugendwiderstandsfähigkeit wird durch nekrogene, die Alterungswiderstandsfähigkeit durch plasmatische Abwehrreaktionen verursacht. Dieser Phasenwechsel gilt für alle Befallstypen der untersuchten *Ribes*-Arten. Unter-

schiede bestehen nur in der Stärke der nekrogenen und plasmatischen Abwehrreaktionen, in der Zeit ihres Einsetzens, der Dauer ihres Wirkens und in ihrem Erfolg dem Parasiten gegenüber. Von den beiden befallsfrei bleibenden *Ribes*-Arten reagiert *R. divaricatum* Dougl. vorherrschend hypersensibel (Resistenztyp:0), *Ribes niveum* D. dagegen vorherrschend normergisch im Sinne von GÄUMANN (Immuntyp:1). Im ersten Falle bleibt die nekrogene Reaktionsform bis zum Einsetzen der Alterungsresistenz erhalten. Im zweiten Falle setzen normergische Effekte schon im Streckungsstadium der Epidermien ein, die eine Weiterentwicklung der Impfsporen verhindern.

Bei Anwendung von Pilzpopulationen (Ascosporeninfektion) ist bei allen Wirten des Befallstypus 0 bis 3 anhand abweichender Befallsanalysergebnisse das Auftreten physiologischer Rassen nachweisbar. Von 20 Neuzüchtungen verhalten sich 18 wie *Ribes divaricatum* Dougl. das eingekreuzt ist (F4). Zwei der Neuzüchtungen blieben auch bei Anwendung landfremder Pilzpopulationen befallsfrei (Immuntyp).

Die Untersuchungen erbringen den Nachweis, dass der Parasitismus von *Sphaerotheca mors uvae* auf den verschiedenen *Ribes*-Arten ein aussergewöhnlich günstiges Untersuchungsobjekt darstellt, dessen weitere Bearbeitung nicht nur im Rahmen pflanzenzüchterischer Aufgaben, sondern auch in theoretischer Hinsicht wertvolle Einblicke in verschiedene phytopathologische Fragestellungen geben wird.

G. VIENNOT-BOURGIN (Paris)

Etude morphologique de quelques lésions charbonneuses des végétaux

La limitation du parasitisme des charbons nus ou vêtus aux organes floraux n'est pas absolue. La stérilisation préalable de l'épi par envahissement des bractées internes à l'aide de *Fusarium culmorum* ou *Trichothecium roseum*, est capable de provoquer l'apparition de tumeurs foliaires pour *Ustilago tritici*, ces tumeurs existant spontanément pour *U. nuda*

et *U. avenae*. De telles anomalies dans la localisation des sores permettent de concevoir une transition entre les charbons d'ovaires et d'enveloppes florales et certains charbons de feuilles tels que *U. maydis*.

En même temps on constate un traumatisme généralisé à l'ensemble de la plante (nanisme). Ce phénomène se trouve cependant peu accusé par suite de la courte durée du support (*Ustilago nuda* et *U. bromivora*). Ce second effet du parasitisme des *Ustilaginales* cécidiogènes n'en constitue pas moins une relation entre le mode d'action parasitaire des maladies charbonneuses des végétaux annuels et des *Ustilaginales* qui s'attaquent aux plantes vivaces monocarpiques ou polycarpiques pour lesquelles s'établit la pérennance mycélienne. Dans ce dernier exemple, le traumatisme devient généralisé et le développement foliacé exagéré de l'hôte, toujours stérile, facilite constamment la conservation et l'extension du parasite. Le nanisme correspond plutôt à une prolifération de tiges faibles et anormales (cas de *Ustilago holci-*

avenae) tandis que le gigantisme (*Ustilago hypodytes*) est la conséquence de l'étirement de l'axe floral.

En fonction de l'espèce parasite, le développement de la cécidie florale se réalise suivant deux faciès. Dans le premier, seules les étamines constituent le support des amas de chlamydospores, les autres pièces florales externes ne manifestent alors pas d'anomalie sensible (*Ustilago* du groupe *violacea*). Dans le second cas, les organes de la fleur dans leur ensemble, sauf cependant les étamines, participent à l'accumulation sporifère. Ces étamines persistent, demeurent fertiles et manifestent souvent une elongation remarquable qui leur confère un rôle dans la consolidation de la cécidie (hétérostylie chez *U. ovalidis*, épaississement des filets staminaux pour *Sorosporium punctatum*). Du fait de leur soudure basilaire partielle, les étamines sont aussi capables de jouer un rôle mécanique pour la déhiscence des cécidies ovariennes (*Sorosporium loudetiae*).

SESSION 3

Jointly with Section AGR: July 14th, 1—4 p. m., Attendance: 140 members

Chairman: W. RUDORF, Records: K. BJÖRLING and E. ÅKERBERG

SUBJECT:

Resistance Problems from a Genetical and Phytopathological Point of View. General Topics

E. C. STAKMAN (St. Paul, Minn.)

Variation in Plant Pathogenic Fungi and its Practical Importance

There are many biotypes within species of most plant pathogenic fungi, and evidence is accumulating that this is true of phytopathogenic bacteria and viruses also. In the fungi, physiologic races are recognized as comprising one or more biotypes differing principally in physiologic characters, including pathogenicity.

Attempt has been made to ascertain the number, distribution, mode of origin, and practical importance of these races. Studies on cereal rusts and smuts have supplemented each

other in such a way as to establish general principles.

Within some varieties of *Puccinia graminis*, *tritici* and *avenae*, there are many races that differ from each other in their ability to attack certain crop varieties. Within the variety *tritici* approximately 250 races have been recognized, 189 of which have been described. Some races comprise biotypes that differ in minor characters of pathogenicity on varieties now available. As new varieties are produced, differences between biotypes may prove to be more pronounced and single races may be divided into several.

New races of *P. graminis tritici* and *P. gra-*

minis avenae are produced by recombinations in the sexual stage on *Berberis* spp. For more than a decade only four races, 17, 19, 38, and 56, of *P. graminis tritici* have been of importance in the Upper Mississippi Valley of the United States of America, from which most of the barberries have been eradicated. When isolates were made near rusted barberries in Eastern United States in 1949, however, 43 distinct races and biotypes were obtained from a local area. Some of these races were much more virulent than the prevalent ones, and it seemed likely that some of these virulent races might extend their geographic range and increase in prevalence. This happened in 1950, when race 15 B, the most virulent race of wheat stem rust ever found in North America and which had been found principally near rusted barberries, became widely prevalent and destructive on hitherto resistant varieties in northern United States. Concurrently, race 7 of oat stem rust, which attacks certain hitherto resistant varieties, became equally widespread and prevalent.

Ustilago zeae (*U. maydis*) is a good morphological species that comprises innumerable biotypes. The writer and colleagues studied approximately 7 500 biotypes within this species, all of which were derived as mutants or recombinations from two original sporidia. Many biotypes differ from each other in minor characters that would not be recognized in obligate parasites like the rusts and mildews.

Some biotypes of *U. zeae* are extremely mutable, while others are relatively stable, and produce innumerable new biotypes as a result of mutation. The smut fungi therefore are among the most suitable of phytopathogenic fungi for study of mutations and recombinations. Not all of the smut fungi are as mutable as *U. zeae*. Even though they may be relatively non-mutable, however, new combinations can result from hybridization between biotypes within a species, between races within species, between species, and between genera.

The smuts and the rusts are especially suitable for studying variations and its consequences, but the same phenomena have been

observed in many other phytopathogenic fungi studied by the writer and his colleagues. Clearly, most phytopathogenic fungi comprise physiologic races, new ones are continuously being formed as a result of hybridization and mutation, and occasionally races virulent to hitherto resistant varieties are produced, become prevalent, and attack varieties that were resistant prior to the advent of new races.

Discussion

W. RUDOLF: Does the selection of resistant varieties promote the appearance of new aggressive races hitherto unknown?

E. C. STAKMAN: I don't think so; it may, however, permit certain virulent races to multiply without competition from other races to which the variety is resistant. The resistant variety, therefore, by screening out certain races enables the virulent race actually to multiply more rapidly because of lack of competition.

K. O. MÜLLER: Durch das permanente Auftreten neuer oder scheinbar neuer Rassen pflanzenpathogener Pilze hat im letzten Jahrzehnt die Resistenzzüchtung fühlbar an Kredit verloren. Eine extrem negative Kritik geht dahin, dass es, auf die Dauer gesehen, ein fruchtloses Unterfangen wäre, auf diesem Wege die Ernteverluste einzuschränken, die wir z. B. alljährlich im Getreidebau infolge Rostbefalls unserer Bestände zu beklagen haben. Diese Auffassung ist zweifellos abwegig. Auf jeden Fall wird dem Parasiten auch durch die Züchtung von nur teilresistenten Sorten, zumindest zeitweilig, das Leben erheblich erschwert. Man stelle sich nur vor, dass alle z. Zt. realisierten und von der Natur noch in Reserve gehaltenen Rassen der drei Weizenroste in jeder Weizensorte ein offenes Haus vorfinden würden. Ich glaube, die Ernteverluste wären unter diesen Umständen noch erheblich höher, als sie es schon ohnedies sind. Eine gütige Fügung hat nun einmal dafür gesorgt, dass beide Parteien, Wirt und Parasit, auf ihre Rechnung kommen. Vom Standpunkt des Züchters aus gesehen, heisst das aber — wenn wir einmal in abgewandelter Form ein

deutsches Sprichwort an —: Wohl hat der Herrgott die Bäume wachsen lassen, doch hat er weislich dafür gesorgt, dass sie mit ihren Kronen nicht den Himmel streifen.

G. W. KEITT (Madison, Wis.)

Inheritance of Pathogenicity in Venturia inaequalis

This paper reports aspects of a series of studies by the author and associates on apple scab and its inciting fungus, *Venturia inaequalis* (Cke.) Wint., an eightspored Ascomycete. Genetic purity, adaptability, and control of experimental materials are of prime importance. Each line of fungus employed stemmed from a single haploid nucleus. The following adaptations of the experimental materials have been shown: This pathogen freely infects young, vigorous, unwounded tissues and may live for weeks in intimate association with living host cells. It has many biotypes with different pathogenic capabilities to different host species and varieties. It can be cultured through its life cycle and bred *in vitro*. It is haploid throughout the parasitic phase and in its vegetative stage *in vitro*, thus permitting study of effects of a single set of genes. The ascus contains the complete progeny stemming from a single meiosis, with survival of all nuclei in an orderly arrangement that permits tracing the line of nuclear descent by isolating the ascospores in their serial order and studying the derived cultures. Vegetative cells are uninucleate and free from important problems of heterocaryosis. The fungus responds well to mutagenic agents.

Only two main types of disease reaction have been encountered with wild-type lines of the fungus inoculated to apple leaves, "lesion" (typically pathogenic) and "fleck" (non- or slightly pathogenic). Any wild-type fungus line may incite the lesion reaction with one apple variety and the fleck with another. For studying inheritance of pathogenicity lines of fungus and varieties of host giving desired disease reactions are selected and environment throughout the experiments is controlled in a range to

permit normal developments. In all cases adequately studied segregation of factors controlling pathogenicity, as indicated by the lesion or fleck reaction, has occurred in 1:1 ratio alternatively in the first or second nuclear division in the ascus. It has been shown that pathogenicity of two lines of the fungus to two apple varieties is controlled at one locus and to two other varieties at another locus, and that these two loci segregate independently. Certain cultural mutant genes have been shown to suppress symptom expression without changing the gene conditioning pathogenicity. Numerous mutants have been induced experimentally and studied genetically. Correlated studies on the genetics, nutrition, and pathogenicity of this fungus are in progress.

D. J. WATSON (Rothamsted)

Effects of Infection with Beet Yellows Virus on Growth and Carbohydrate Metabolism of Sugar Beet

In field experiments on sugar beet in 1945 and 1946, yellowing of the leaves began about one month after infection with beet yellows virus. At the same time, dry matter yield and total leaf area of infected plants began to fall below that of healthy plants.

In the period August–October, 30–40 % of the leaf area of infected plants was yellowed in 1945, and 35–45 % in 1946.

Total leaf area was reduced by 30 % in 1945 and by 20 % in 1946. Leaf number per plant was not decreased by infection; the reduction of total leaf area was therefore due to decreased leaf size. Infection reduced Net Assimilation Rate, calculated on total leaf area, by 18 % in 1945 and 44 % in 1946. When calculated on the area of leaf surface remaining green, NAR was unaffected by infection in 1945, but was decreased by 18 % in 1946. This may indicate that yellowed leaves of infected plants made little or no contribution to dry matter production, and that, in 1946 infection also reduced photosynthesis in leaves that remained green. There was less sunshine in August and September in

1945 than in 1946, and this may account for the smaller reduction of NAR and less severe yellowing, for shading has been found to reduce symptoms of virus yellows.

Loss of dry matter yield caused by infection (35 % in 1945, 43 % in 1946) was evidently the result of decreases in both NAR and leaf area; in 1946 the effect on NAR was the greater, but in 1945 leaf area was more severely affected than NAR. The effect of infection on leaf area cannot, therefore, be attributed wholly to a reduction in the amount of assimilate available for growth.

Previous workers concluded from the occur-

rence of "phloem gummosis" in yellows-infected plants, and from results obtained by the Sachs iodine test, that starch accumulates in infected leaves because translocation is inhibited by blockage of the sieve-tubes. Determinations of starch and sugar content have shown, however, that loss of starch and of total carbohydrates per cent of residual dry matter during a dark period was as great from infected as from healthy leaves. Infected leaves had a higher content of sucrose and reducing sugars, as well as starch, than healthy leaves. The greatest increase was in reducing sugars; they account for 20 per cent or more of the dry matter of infected leaves.

SESSION 4

Jointly with Section FOB: July 17th, 9 a. m. — 1 p. m., See page 294

SESSION 5

Jointly with Section AGR: July 17th, 2—6 p. m., Attendance: 150 members

Chairman: F. C. BAWDEN, Recorders: K. BJÖRLING and E. ÅKERBERG

SUBJECT:

General Virus Problems

F. C. BAWDEN (Harpenden, Herts.) *Some Properties of the Tobacco Necrosis Viruses*

The name tobacco necrosis was used by SMITH and BALD in 1935 for a virus disease of tobacco seedlings that presented several unusual features. Symptoms were restricted to the two first-formed leaves, which lie on the soil. The upper leaves were not only symptomless, but also virus-free, although they developed local lesions when inoculated with sap from the lower ones. Essentially the same disease can be caused by several serologically unrelated viruses, which also differ from one another in stability and particle size. Each virus may occur in a number of strains, distinguishable either by the lesions

they cause in certain hosts or by their behaviour *in vitro*.

The viruses have extensive host ranges and are often present in the roots of many plant species that have shown no symptoms. They have been found in many countries, and appear to be soil-borne, but how they are maintained in soil is unknown. In most plants, whether or not they cause necrotic lesions, they do not become systemic. Only this fact prevents them from causing extensive losses, for their potentialities as pathogens are shown by the lethal diseases they have been found causing in tulip and French bean (stipple-streak).

In Britain the disease is much more prevalent in tobacco seedlings during winter than during summer; the seasonal variation may be cor-

related with the fact that reduced illumination increases the susceptibility of leaves to infection.

From plants infected with several of the tobacco necrosis viruses, seemingly homogeneous preparations of crystalline nucleoproteins have been made. One isolate (the Rothamsted culture) has differed strikingly from the others. It has never crystallized when precipitated with ammonium sulphate, and treatments without effect on others cause it to lose infectivity. Highly infective preparations contain two specific particles, with diameters of about 17 m μ and 34 m μ respectively. The small particles crystallize when sedimented by ultracentrifugation and from concentrated salt-free preparations. Homogeneous preparations of the small particles have little infectivity, but are highly active serologically. The large particles may be aggregates of the smaller ones, but this is not established. Some increase in infectivity occurs after the virus is extracted in sap; whether this activation is produced by changes in the structure of virus particles or by the destruction of inhibiting substances is unknown.

Discussion

E. VAN SLOGTEREN: We found this disease as early as 1924 on a big scale on a field that had been planted with potatoes. We often find it after a crop of potatoes or tobacco but could not find a transmission with the bulbs. CASANIS found it in England in plants grown under glass and I have to suppose that these tulips have got the disease from the soil—infected by another crop?

MARIA DE BRUYN OUBOTER: Answer to Dr. BAWDEN's remark that tulips could not be artificially infected with tobacco necrosis virus in the soil. We succeeded in Lisse to infect tulips by putting pieces of diseased tobacco leaves into the soil above the newly planted tulip bulbs. Separating the roots from the growing leaves by a layer of paraffin we made sure that the infection took place through the young leaves probably when the leaves are wounded in growing through the soil.

R. BEST, K. SILBERSCHMIDT and F. C. BAWDEN had a discussion, from which no written contributions were delivered, on the influence of the degree of dispersion of the various preparations of tobacco necrosis virus on their infectivity.

C. H. CADMAN and R. V. HARRIS (East Malling, Kent)

Recent Advances in Research on Raspberry Virus Diseases

None of the viruses known to infect wild and cultivated raspberries in North America and Britain has proved to be transmissible by mechanical methods of sap inoculation, nor has any been transmitted to hosts outside the genus *Rubus*. Work in America and recent work in Britain suggests that the aphid *Amphorophora rubi* Kalt. is the principal vector of these viruses, in the field, in both countries.

The analysis of the virus complexes causing the economic diseases in Britain was at first limited to deductions from graft transmissions to a range of commercial varieties of red raspberry selected as indicators; but these have all proved to have marked though varied limitations in the range of diagnostic symptoms they will express. Latterly, however, the use of *Rubus saxatilis*, *R. henryi*, and *R. occidentalis* has greatly clarified the information thus accumulated.

Existing results from these experiments can be explained on the assumption that:—

(a) there are six distinct viruses or virus strains responsible for the vein-banding (Mosaic 1) vein-clearing and yellows symptoms found on Norfolk Giant, St. Walfried, Baumforth B and other indicator varieties.

(b) there are a further 6 or 8 distinct viruses or virus strains responsible for the Mosaic 2 disease expressed by Norfolk Giant, St. Walfried and Baumforth B, but not by Lloyd George, Malling Seedling varieties and others.

(c) there are three distinct viruses responsible for the leaf curl and blotch disease of Norfolk

Giant and Lloyd George respectively, and for the *Rubus* Stunt disease.

(d) there is a residue of two or more "latent" viruses present, without apparent effects, in stocks of Norfolk Giant and other cultivated varieties, and in wild raspberries. And there is evidence that this formidable list of some seventeen viruses is not yet complete.

No particular significance should be placed on their present grouping, which is made almost entirely on the results of grafting experiments. Any classification based on similarities in symptom expression, such as for example occurs among the viruses of the Mosaic 2 group, must be regarded as tentative until the etiological relationships of each of the viruses to the economic diseases have been determined. For example one or more Mosaic 2 viruses can invariably be detected in degenerate but symptomless stocks of Lloyd George, but other viruses are also present, and the healthiest known stocks contain a "latent" virus. So that until the virus content of degenerate stocks can be accurately analysed by means of differential aphid transmission, the exact interrelations of these and the other viruses, and the role of each virus in such failure, cannot be finally assessed.

The final resolution of the causal viruses involved awaits the application of finer methods of analysis such as that depending on differing relations between the viruses and the insect vectors. The latter method, however, has been impracticable because of the high resistance of the indicator varieties of red raspberry to infection by aphids, a phenomenon due to factors at present unknown. But more rapid progress is possible now that the two indicator species *R. saxatilis* and *R. occidentalis* have proved highly susceptible to infection by this means.

Discussion

N. F. BUCHWALD: Have you investigated the virus diseases of the wild growing raspberries in forest and found some of the same virus types as in the cultivated ones? If so the wild growing raspberries must present a great risk for cultivating raspberries.

R. V. HARRIS: We are aware of the importance of wilding raspberries as potential sources of virus infection particularly in Scotland where they are so prevalent. In the neighbourhood of cultural areas what appear to be wildings are frequently "escapes" from cultivated stocks and these frequently and generally show severe virus symptoms. In the upland areas symptoms are less frequently seen but recent tests have shown that these wildings are frequently infected with viruses, including the so-called Norfolk Giant latent virus.

L. M. BLACK (New York)

Multiplication of Clover Club-Leaf Virus in Its Insect Vector

The clover club-leaf virus, *Aureogenus clavifolium* Black, passes through the egg of its leafhopper vector, *Agallioptis novella* Say. On February 8, 1945, a virus-bearing female weighing 1.7 mg was mated with a virus-free male and the pair caged on a Grimm alfalfa plant, *Medicago sativa* L. Alfalfa is immune to the virus. The female produced 42 nymphs, of which 21 were tested individually on a series of crimson clover plants, *Trifolium incarnatum* L. and then discarded. Fifteen of the 21 produced infections. Therefore, on the average, the virus in the original female had been diluted approximately 1:30 among her progeny. The 21 remaining progeny were each placed on an alfalfa seedling and when they became adults, the females were mated to virus-free males. In a similar manner, the experiment has been continued for more than 5 years through 21 generations of insects grown only on immune alfalfa without loss of infectivity. The dilution of the original virus, assuming no multiplication in the insects, exceeded 1 to 2.8×10^{26} . Even a mass of hydrogen weighing the same as the original female (1.7 mg) consists of only about 5.1×10^{20} molecules. Therefore, the virus must have multiplied in its insect vector.

The virus has a long incubation period in both insect and plant and in each generation insects had to be mated before any infectivity

data were obtained on their sibs. In each generation the pair that produced the greatest number of progeny was chosen for the main line of descent. Ordinarily, in each generation, a sample of about 15 progeny from each of 5 families was tested individually on crimson clover to determine the fraction that was infective. Another sample of about 10 nymphs from each of the same 5 families was distributed, one nymph to each of a number of alfalfa plants, to provide females for continuing the line.

The clover plants on which the samples of insects from the main line were tested were matched in each generation with at least as many control plants, none of which became infected. The soil used was steamed to kill seeds and since weeds never grew in the pots in which the alfalfa plants were caged the alfalfa was the only source of food for the insects. After the alfalfa plants had been freed of leafhoppers, they were tested for the virus by means of virus-free insects. After feeding on the alfalfa plants for a month, these insects failed to infect any of 431 clover plants, whereas comparable insects after feeding on diseased clover infected 148 of 406 plants.

That the club-leaf virus multiplies in plants was shown by 30 graft passages of the virus in series through *Vinca rosea* L. The virus is therefore capable of self-replication in both plant and insect hosts and in this sense is both a plant and an animal virus.

Discussion

F. C. BAWDEN pointed out that in his opinion Dr. BLACK's results must be interpreted as the first real evidence of a multiplication of a plant virus in its insect vector.

R. BEST: If Dr. BLACK's conclusions stand up to the test of time, as I believe they will, they are of such fundamental importance that other implications might be profitably examined.

R. BEST, MARION WATSON, P. H. GREGORY and L. M. BLACK had a discussion, from which no written contributions were delivered, on the mechanism of this type of virus multiplication;

whether the results indicated a multiplication at the expense of some constituents of the insect itself or of some plant constituents absorbed by the insect; and, secondly, on the question of the transport of the virus from the stomach of the insect to the egg of the young and back to the stomach of the young.

E. KÖHLER (Celle)

Beitrag zum Prämunizitätsproblem; Studien am Tabakmosaik

Wenn man das Virus des Paratabakmosaiks (PTM) auf gesunde Blätter des White Burley-Tabaks aufreißt, so erzeugt es an diesen ausgedehnte nekrotische Infektionsherde. Verimpft man dasselbe Virus, das eine stärker abweichende Variante des Tabakmosaik-Virus (TMV) vorstellt, in derselben Weise auf junge Blätter älterer White Burley-Pflanzen, die früher mit dem gewöhnlichen TMV infiziert wurden und deren Blätter eine klare Sonderung in hellgrüne und dunkelgrüne Bezirke erkennen lassen, so bilden sich diese nekrotischen Herde ausschliesslich auf den dunkelgrünen, niemals aber auf den hellgrünen Bezirken. Selbst auf kleinsten, isoliert stehenden dunkelgrünen Flecken können die nekrotischen Herde auftreten. Die hellen Bezirke sind also abwehrfähig (prämun), die dunklen nicht. Die mangelnde Prämunizität der dunklen Bezirke beruht offenbar darauf, dass sie eine virusfreie Epidermis und ein wenigstens teilweise virusfreies Parenchym besitzen. Dieser Umstand ermöglicht es dem aufgeimpften PTM-Virus, sich in ihnen zu vermehren und auszubreiten. Die hellen Bezirke sind hingegen prämun, weil sich das aufgeimpfte PTM-Virus in ihnen nicht vermehren kann; die Baustoffe sind bereits durch das TMV aufgebraucht. Die Annahme einer aktiven Abwehr ist nicht erforderlich.

Wenn man die Preßsäfte aus hellen und dunklen Bezirken auf ihren Gehalt an TMV-Virus vergleichend untersucht, so findet man, dass die dunklen Teile annähernd 60 % weniger enthalten als die hellen. Es ist bemerkenswert, dass sich dieses Verhältnis auch im ausge-

wachsenen Blatt nicht verändert. Dieser Befund spricht gegen die Möglichkeit eines Übertritts des TM-Virus in die von vornherein virusfreien Gewebeteile. Als virusfrei sind die beiderseitige Epidermis und das Assimilationsparenchym anzusehen, während Schwammparenchym und Leitgewebe das Virus enthalten. (In den hellen Bezirken enthalten die Haare reichlich Viruskristalle und zwar fast regelmässig in jeder Zelle; sie fehlen fast ebenso regelmässig in den Haarzellen der dunklen Bezirke. Die satte Grünfärbung des Assimilationsgewebes deutet auf ein Freisein von Virus hin.)

Es ist nach Vorstehendem anzunehmen, dass schon auf einem frühen Entwicklungsstadium unter dem Einfluss der Virusinfektion ein Verschiessen oder Unwegsamwerden von Plasmaverbindungen eintritt, wodurch das Vordringen des Virus in die genannten Gewebepartien verhindert wird.

Am ausgewachsenen Blatt erlischt die Infizierbarkeit der dunklen Bezirke, jedoch ist es fraglich, ob diese Erscheinung als Folge einer verspäteten Abwehrreaktion gedeutet werden kann. Gegen diese Deutung spricht die Tatsache, dass vorhandene PTM-Infektionsherde sich auch am ausgewachsenen Blatt noch stark vergrössern, was auf eine ungehinderte Virusvermehrung an den Rändern der Herde schliessen lässt. Deren Wachstum macht an den Zonengrenzen nicht einmal regelmässig Halt, sondern überschreitet zuweilen sogar noch diese Grenzen. Jedoch bedarf diese Erscheinung noch einer genaueren Analyse.

A. ROZENDAAL, T. H. THUNG and
J. P. H. VAN DER WANT (Wageningen)
Soil-Borne Virus Diseases

The potato disease called "kriengerigheid" in Holland ("sprain" or "spraing" in England, "taches en couronne" in France and "Propfenbildung" in Germany) affects only the tubers, which on cutting show concentric brown necrotic rings, having their centre somewhere in the neighbourhood of the surface.

As suggested by PETHYBRIDGE (1912/13) and

QUANJER (1926), it seems that here infection has taken place. Attempts to prove a bacterium or fungus as cause of the disease have thus far failed.

One of the striking properties of the trouble is that it is confined to certain soils, in sandy and peaty regions, whereas in clay districts it is found only in places where the soil contains sand.

QUANJER (1926) proved that the steaming of soil from plots where it occurs acts as a means of disinfection. ATANASOFF (1926), working in his laboratory, grafted parts of young healthy tubers of plants growing on sick soil, but later workers failed to corroborate this infection experiment. QUANJER correlating the non-fungoid and non-bacterial nature of leafroll, mosaic and related diseases with the evidence of superficial entrance in the tubers suggested the possibility of a virus origin. He further proved that potato varieties differ markedly in susceptibility.

In Holland a new impetus to further investigation was given by ROZENDAAL (1947), ROZENDAAL and VAN DER WANT (1948). They found that the stem-mottle disease of potatoes occurring in the Netherlands, and a systemic disease of tobacco called "Streifen- und Kräuselkrankheit" in Germany (BÖNING 1931), "ratelziekte" ("rattle-disease") in Holland (QUANJER 1943) and "Streg-Krøllesyge" in Denmark (HANSEN, 1946), are caused by the same soil-borne virus. A characteristic of this disease is that in tobacco sometimes the new shoots and in potato some tubers escape infection.

Not always potatoes planted on sick soil show symptoms in the leaves, but it has been stated that in such cases, where infection may have occurred, part of their progeny shows "stem-mottle" when grown the following year on healthy soil.

Another feature of the disease is that it is not readily transmitted by stem grafting. Up to this moment it has remained impossible to transmit the disease by tubergrafting. The infectious nature of the disease, however, is easily demonstrated by rubbing sap from stem-mottle diseased potato leaves into tobacco where it

produces (if conditions are favourable) ring-like necrotic spots after 5 days and, later on, symptoms of the rattle disease, when virus becomes systemic. On the other hand inoculation of potato leaves with sap from stem-mottle leaves or rattle diseased tobacco plants only results in a few necrotic spots and some spreading of necrosis along the leaf stalk. Systemic symptoms do not appear and the progeny of such inoculated potato plants gives only rise to virusfree plants. Probably nature inoculates in another way than we did.

Sprain and stem-mottle have many similarities. So it is a marked fact that potato varieties which are susceptible to one of the diseases are also susceptible to the other, whereas those which are resistant to the first are also resistant to the second.

In 1948 we carried out an experiment with tobacco and potatoes on peaty soil near Sappemeer (Groningen), where stem-mottle in potatoes was often observed. With only a few exceptions, all tobacco plants remained healthy and no symptoms of stem-mottle were seen in the leaves of the potato plants. Nevertheless many tubers showed heavy necrosis resembling closely typical sprain, often accompanied by sunken spots on the tubers. These tubers have been cultivated in 1949 on the experimental field of the Laboratory for Phytopathology at Wageningen. This field has been under cultivation during more than 25 years and up till then here potatoes never became infected with sprain or stem-mottle.

However, in the progeny of the plants grown in Sappemeer, about 25 % showed stem-mottle, whereas 20 % of the plants had formed one or more tubers showing heavy sprain. This experiment has given full evidence that sprain is an infectious soil-borne disease. Although it was found in former experiments that sprain may be transmitted by seed potatoes exceptionally and to a low percent, in the last-described experiment the transmission was evident and the severity of the symptoms indicate that we had to do with a very pathogenic strain of the disease agent. It is not proved by these experi-

ments that the agent is a virus, but the fact that stem-mottle and sprain have much in common makes it highly probable that also sprain is caused by a virus.

In the Netherlands soil-borne virus diseases belonging to the tobacco necrosis group occur, e.g. stipple-streak of bean (BAWDEN and VAN DER WANT, 1949) and a necrotic disease of tulips (DE BRUIJN OUBOTER and VAN SLOGTEREN, 1950). Recently a tobacco necrosis virus has been isolated from mosaic diseased carnation (NOORDAM, THUNG and VAN DER WANT, 1950). This type gives rise to local necrosis on tobacco and beans. Later on it becomes systemic but in beans only. On carnation itself it induces a systemic mosaic.

Former work, carried out especially in America, had already given full evidence of the economic interest of soil-borne viruses of different types (MACKINNEY, 1946). In Europe, however, this has been shown only in recent time. New problems are associated with these viruses, viz. regarding the state in which they occur in the soil, the possibility that there are special vectors which favour their hibernation and the way in which control measures should be conducted.

A. ROZENDAAL, T. H. THUNG and
J. P. H. VAN DER WANT (Wageningen)
Curing Virus Diseases by Heat

Successful treatments of virus diseased plants by heat have been reported by WILBRINK (1923) with regard to sereh disease of sugar cane, by KUNKEL to yellows, red suture, little peach and rosette of peach (1936), aster yellows of *Vinca rosea* and *Nicotiana rustica* (1941), false blossom of periwinkles (1942), potato witches' broom (1943) and by DUNKELMAN, LUKE, GIBBINS and EDGERTON (1946) to chlorotic streak of sugar cane.

Recently KASSANIS (1949) published the results of his experiments on the curing of potato leaf-roll by heating tubers from diseased potato plants during at least 3 weeks at a temperature of about 38° C.

In our experiments carried out during the autumn and winter 1949-1950 root cuttings from mosaic diseased raspberries were heated for 30 min. in waterbaths of 13°, 40°, 45°, 50°, 55° and 60° C. Directly after the treatment the cuttings were potted. All cuttings treated at temperatures of 50° C and higher proved to be killed; those treated at 45° C formed quicker sprouts than those of the check treatment (13° C). When they grew older, symptoms of mosaic became distinct, thus providing evidence that this treatment had no effect on this disease.

Other cuttings were immersed during 30, 60, 90, 120 min. in water of 45° C; they proved to resist treatments up to 60 min.; longer treatments gave serious damages. Other experiments were also carried out in such way that cuttings of mosaic diseased raspberries were placed in moist sand or moss during 4 days in a incubator at 40° C. Most cuttings deteriorated but those which remained alive developed leaves with symptoms of the disease. So we conclude that heat treatment is not successful in curing raspberry of mosaic. Heat treatment for witches' broom of this plant was more satisfying.

This disease shows dwarfing and excessive outgrowth of axillar buds. After two or three years the diseased plant consists of a dwarf bush of short root shoots and axillar buds which are grown out with small leaves.

RIETSEMA (unpublished) gave proof by grafting that this disease is caused by a virus. It is not yet known whether it is the same disease as described by PRENTICE and HARRIS (1950).

In our experiments diseased plants were divided into 4 parts, which were planted in pots; 2 pots were placed in the greenhouse, whereas the 2 others were kept in an incubator at 40° C for 4 days. Afterwards they were also brought to the greenhouse. The treated parts formed new normal looking shoots, whereas the untreated ones remained dwarfed. Later on, in the hot season when the temperature in the greenhouse became rather high (up to 36° C) during several weeks, also these check-parts grew to normal looking shoots. The plants placed outside the greenhouse remained diseased.

These experiments, repeated with several varieties of raspberries, gave proof that heat curing against witches' broom is possible. The incubator was kept in moist condition and the pots were watered daily. To keep the plants longer in the incubator, i.e. 5 or 6 days, mostly results in killing them.

In another experiment potato tubers infected with several viruses were treated in the same incubator of 40° C. Seven varieties infected with leaf-roll virus, three with stem-mottle virus, one with virus X, one with aucuba virus, one with virus A, one with virus Y, one with both leaf-roll and aucuba viruses, and one infected with both leaf-roll and virus A, were kept in the incubator during times ranging from 12 to 44 days. Units ranging of from 12 to 56 tubers of each variety were thus treated. The results indicate that in some cases potato tubers had become free from leaf roll after a treatment of 12 days. Better results were obtained with some varieties than with others and when the time of treatment approximated the maximum. None of the other virus diseases were cured by the heat treatment. So KASSANIS' results have been confirmed.

The progeny of all cured plants have to be observed further. Many tubers were damaged by the treatment probably owing to the late season when they were already weakened.

Discussion

E. VAN SLOGTEREN: We have tried for many years to inactivate the virus in bulbs by all kinds of heat treatment. The resistance of the plant is very much depending on the pre-treatment of the bulbs. We could make the plants free from symptoms for one year, but later they always proved to be still infected.

H. ROSS: Die Ergebnisse Dr. THUNGS über die Hitzeheilung von Kartoffelknollen vom Blattrollvirus können durch Versuche in Voldagsen bestätigt werden. Ich konnte blattrollkranke Knollen von Juli, Allerfrüheste Gelbe und Mittelefrühe vom Blattrollvirus befreien. Ebenso ist zu bestätigen, dass die Mosaikviren durch dreiwöchige Erhitzung der Knollen auf 38° nicht

Virus Diseases

Disease Common name	Date	Investigators, Country	Scientific name of Virus	
			Fawcett's	Holmes'
Infectious Chlorosis	1913	Trabut, Algeria	Citri- <i>vir</i> psorosis	Rimocortius psorosis
Infectious Mottling	1931	Petri, Italy	C. italicum	Marmor italicum
Scaly bark A	1933	Fawcett, U.S.A.	Citri- <i>vir</i> psorosis var. vul- gare	Rimocortius psorosis var. vulgare
Scaly bark B	1933	Fawcett, U.S.A.	C. ps. var. anulatum	R. ps. var. anulatum
Concave gum	1938	Fawcett & Klotz, U.S.A.	C. ps. var. concavum	R. ps. var. concavum
Blind pocket	1941	Fawcett, U.S.A.	C. ps. var. alveatum	R. ps. var. alveatum
Crinkly leaf	1943	Fawcett & Bitancourt, U.S.A. & Brazil	C. ps. var. rugosum	R. ps. var. rugosum
Infectious Variegation	1939	Fawcett & Klotz, U.S.A.	C. ps. var. rugosum	R. ps. var. rugosum
Stubborn Disease	1944	Fawcett, Perry, Johnston	C. pertinaceae	R. pertinaceae
Acorn Disease	1944	Haas, Klotz, Johnston	C. pertinaceae	R. pertinaceae
Little leaf Disease	1927	Reichert & Perlberger, Palestine	C. pertinaceae	R. pertinaceae
Tristeza	1946	Meneghini, Brazil	Citri- <i>vir</i> viatoris	Corium viatoris
Quick Decline	1946	Fawcett & Wallace, U.S.A.	Citri- <i>vir</i> viatoris	Corium viatoris
Virus disease of lime	1949	Hughes & Lister, Gold Coast	Citri- <i>vir</i> viatoris	Corium viatoris
Bark shelling Trifoliolate Orange	1948	Benton et al., Australia	C. exocorte	Rimocortius exocorte

zerstört wurden. Dies betrifft das Virus X^B in Erstling, C in Carla und A in Juli und Allerfrüheste Gelbe. — Mit Hilfe der Blattrolltestpflanze *Physalis Florida* konnte Frl. Dr. BAERECKE entscheiden, ob die hitzebehandelten Knollen tatsächlich blattrollfreie Stauden lieferten. Bisher verliefen die Teste negativ.

F. C. BAWDEN, R. BEST, R. V. HARRIS, K.

SILBERSCHMIDT and T. H. THUNG took part in the discussion that followed.

L. J. KLOTZ (Riverside, Calif.)

Virus Diseases of Citrus

TRABUT in 1913 in Algeria described a graft-transmissible "chlorose infectieuse" of sweet

of Citrus (L. J. Klotz)

Vector	Other means of Inoculation	Varieties attacked Common name	Control
Toxoptera aurantii?	budding grafting	Sweet orange	Use disease-free budwood
	" "	Sour orange	" " " "
	" "	Leaf & bark Symptoms Leaf only	" " " "
	" "	Sweet or. Lemon	Scrape lesions or treat them with
	" "	Grapefruit Lime	DNOCHP (1% in kerosene)
	natural root grafts	Mandarins Sour or.	
	" "	Tangerines	
	" " "	" "	Use disease-free budwood
	" " "	Sweet orange, lemon, & probably other Citrus spp.	" " " "
	" " "	" "	" " " "
	" " "	Lemon	" " " "
	" " "	Lemon, sour orange	" " " "
Aphis citricidus	budding grafting	Sweet orange, grapefruit	" " " "
	" "	" " "	" " " "
Probably Aphis gossypii	" "	Shamuti orange	" " " "
	" "	" "	" " " "
A. citricidus	" "	Sweet orange, mandarin, etc. on	" " " "
	dodder 2/01	Sour orange, grapefruit, etc. See list by Grant & Costa	Grow only tolerant or disease-free combinations
Probably Aphis gossypii	budding grafting	Sweet Orange on	Sweet orange as on Sweet, Trifoliate or
	" "	Sour orange, grapefruit, shaddocks, most lemons, some tangelos Grapefruit on Sour orange	" " " "
A. citricidus	" "	Lime seedlings	Grow limes on Rough lemon stocks
	" "	Trifoliate orange	Use seed & budwood from dis- ease-free sources

orange. The trouble may have been psorosis or the combination effects of psorosis and general starvation from root destruction.

PETRI in 1931 described a "variegatura infetiva" of the leaves of young sour orange. The symptoms are similar to our infectious variegation of lemon although the Sicilian trouble was not found on lemon. Infectious

variegation is readily transmitted to sour orange by budding, however.

FAWCETT in 1933 noted light green elongated clearings or flecks, along the small veins of half grown leaves of Valencia orange. Only trees that either showed bark symptoms of psorosis or had been grown from budwood of parent trees that had psorosis showed this symptom.

It is now used to great advantage by nurserymen to secure budwood free from psorosis. Psorosis has been the most important virus disease of *Citrus* but as a result of this discovery, it may become a minor trouble. No evidence of transmission of this disease by insects has been demonstrated. The only known way thus far is by the union of living tissue. Virus preparations concentrated by means of the ultracentrifuge are being tested.

Six forms of psorosis including psorosis A, psorosis B, concave gum disease, blind pocket, crinkly leaf, and infectious variegation have in common the leaf symptom described. Further evidence of the relationship is that sweet orange budded with crinkly leaf or infectious variegation develop the typical bark scaling of psorosis A. Also blind pocket sometimes produces scales.

Stubborn, acorn, and little leaf diseases, which attack orange and grapefruit are probably caused by the same virus. The symptoms are a patternless chlorosis of leaves which fold upward along the mid-vein, off-blooming, small numbers of fruit, some of which may have an acorn shape and bitter taste, and a general brush-like, bentdown growth of twigs caused by abnormal branching from multiple buds. The albedo of affected grapefruit may be bluish in color. Transmission by budding and grafting has been demonstrated.

Sour orange rootstock incompatibility (ca 1897) and stem-pitting of grapefruit (ca 1948) in South Africa (ca 1897) and in Java (1923), podredumbre de las raicillas in Argentina (1930), tristeza in Brazil (1937) and Uruguay (1940), quick decline in California, U. S. A. (1939), bud union decline in Australia (1948) and virus disease of lime in the Gold Coast (1949) are probably related virus diseases. They may have originated in South African plantings and have travelled in nursery stock and propagative parts to other countries. Because of their effects sour orange as a rootstock in South Africa and Java has failed, the orange plantings in South America have been wiped out, and to date a quarter million navel and Valencia or-

ange trees on this stock have been destroyed in southern California.

The first symptom, and the one which is responsible for the succeeding symptoms is a necrotic breakdown of the sieve tubes in the sour orange bark or other susceptible stock just below the bud union of the trunk. Then follows a destruction of the fibrous roots beginning at the periphery of the root system. The top takes on an appearance of a girdled tree. Leaves become a dull ashen green color and fold lengthwise and upward along the mid-vein; clearing vein is common. Leaves fall and twigs die back, the process apparently keeping pace with root destruction. During periods of soil water deficit young trees will collapse, the leaves suddenly wilting and drying in place, suggesting the name *Quick Decline*. Older trees develop a chronic form.

A large amount of investigation has been made of the reactions of many combinations of scions and rootstocks to tristeza and quick decline. Suffice it to say here that sweet orange and mandarin varieties on sour orange, grapefruit, shaddock, most lemons, and on some tangelos are susceptible, as is grapefruit on sour orange. Of the seedlings three varieties of sour orange, eight grapefruit varieties, four tangelos, six shaddock, four lemons, and three limes have been reported showing symptoms of tristeza.

H. A. GOLD and the writer are attempting to concentrate and purify the *Citrus* viruses for chemical analyses and electron microscopy. Small spherical bodies measuring 13 millimicrons in diameter have been isolated and photographed from psorosis. Purified materials assayed 0.8 per cent phosphorus, based on dry weight, which approximates that of several known virus proteins.

Discussion

K. SILBERSCHMIDT: In many countries sweet oranges are grafted on sour orange stocks on account of the susceptibility of sweet oranges to a fungus disease (foot-rot). Now just this

combination of sweet orange on sour stock proved to be susceptible to the virus of "tristeza" or "quick decline."—I can further point

out that MENEHINI, working in my laboratory in São Paulo, has found a vector of "tristeza disease" already a few years ago.

SESSION 6

July 18th, 9 a. m. — noon, Attendance: 60 members

Chairman: E. VAN SLOTEREN, Recorder: K. BJÖRLING

SUBJECTS:

1) *Growth of Gall Tissues*, 2) *Motion re International Standardization of Technical Words*

P. NOBECOURT (Grenoble)

Cultures de tissus et Phytopathologie

La culture des tissus végétaux a d'étroits rapports avec la Phytopathologie, à la fois dans ses origines et dans ses applications.

C'est en effet, guidé par des préoccupations relatives à des problèmes de pathologie et grâce à des observations faites au cours de recherches sur l'immunité, que l'auteur a pu réaliser les premières cultures indéfinies de tissus végétaux.

Ces techniques ont reçu de multiples applications. Elles ont permis d'aborder par de nouvelles méthodes l'étude d'importants problèmes de Physiologie, d'Histogénèse et d'Organogénèse. Mais elles sont aussi applicables à de nombreuses questions concernant la Phytopathologie.

C'est ainsi que la culture des tissus ou des organes isolés a permis de faire développer *in vitro* des ultra-virus des mosaïques et des champignons parasites obligatoires.

Ce sont surtout les problèmes relatifs aux "cancers végétaux" qui ont donné lieu aux plus nombreuses applications des cultures de tissus; on a ainsi pu mettre en évidence des faits de la plus haute importance pour la connaissance de la nature intime des phénomènes néoplastiques.

Enfin, on peut penser que la technique de culture des tissus végétaux apportera de nouvelles connaissances sur le mécanisme de l'immunité chez les plantes.

A. J. RIKER and A. C. HILDEBRANDT
(Madison, Wis.)

Stimulation or Inhibition by Basic Nutrients of Diseased Plant Tissue Growth Clarified by Studies In Vitro

Many basic nutrients of animal and plant cells are similar. The plants have certain advantages for fundamental work on diseased growth, including (1) low cost, (2) large numbers, (3) easy experimental manipulation, (4) genetic purity or identity through vegetative propagation, and (5) easy tissue culture. Tissue cultures grow indefinitely on synthetic media. Their weight is the measure of growth. Several colleagues were associated with portions of this work.

The origins of four callus tissues used were crown gall on sunflower, marigold, Paris-daisy, and periwinkle. The tissues were free from the causal bacterium, *Agrobacterium tumefaciens* (SMITH and TOWN.) BERGEY *et al.* The tobacco callus came from a hybrid.

The best temperatures and hydrogen-ion concentrations have been studied.

Certain plant extracts have been stimulating or inhibiting, depending on the concentration. Different tissues showed variability in relation to a single extract; and different extracts showed variability in relation to a single tissue. Concentration was often critical. This variability

appeared to be influenced by the balance among common mineral salts, growth substances, and sources of carbon and nitrogen.

Mineral salt balances were examined with over 100 different media. These indicated how much or how little certain changes in salt concentration influence subsequent growth.

With indole, naphthalene, naphthoxy and phenoxy growth substances, the wet weight of sunflower callus usually increased and more scalariform cells appeared at 10^{-7} to 10^{-11} dilutions. At 10^{-3} , the growth was inhibited, and individual cells were larger. Tobacco tissue was not stimulated at the high dilutions but was inhibited at the low dilutions.

As sole sources of nitrogen, urea and nitrate were best for sunflower tissue. Except for arginine, all the amino acids used at about .001 M concentration inhibited growth with nitrate. However, possibly because of transamination, fair growth appeared at .064 M concentration of alanine, glutamic acid, or aspartic acid.

As sole sources of carbon, dextrose, levulose, and sucrose were favorable for growth of all five species. With other sources, the amount of growth often varied. Certain alcohols and salts of organic acids strikingly inhibited specific tissues from growing in the presence of sucrose. Concentration was often critical.

The results came from wet weights of approximately 100 000 pieces of tissue. Some of the metabolites have encouraged growth, while others have slowed or inhibited growth. For normal growth, a number of factors seem to operate in a suitable balance. For diseased growth of one kind or another, these factors may be out of balance in one way or another.

P. MANIGAULT (Paris)

Réactions histochimiques de Pelargonium zonale au cours du développement de tumeurs expérimentales

On sait qu'une inoculation d'une culture jeune d'*Agrobacterium tumefaciens* provoque dans les tissus d'une bouture de *Pelargonium zonale* agée

d'un mois, une prolifération anormale; après une période de latence et de précancérisation il se développe une tumeur qui rappelle en tous points le *crown gall*, maladie naturelle de la plante.

Nous avons étudié déjà l'action d'agents physiques sur le développement de la tumeur expérimentale et pour essayer d'expliquer cette action il nous a paru nécessaire de déterminer d'abord certains caractères histochimiques des tissus sains, et des tissus tumoraux. Nous avons retenu parmi beaucoup d'autres, la répartition de l'amidon, des cristaux d'oxalate, des tannins dans les cellules examinées à différents entre noeuds et en tenant compte des variations dues à la saison. Les résultats obtenus ont été complétés par des dosages d'éléments qui comme les sucres échappent aux techniques usuelles de l'histochimie.

Discussion

G. MOREL: Quel est la durée pendant laquelle il faut faire agir le champ magnétique pour inhiber la formation de tumeur? Il y a-t-il des différences de durée entre différentes espèces telles que celles observés par BRUNN en faisant agir la chaleur sur les tumeurs de Kalanchoe et de Tomato.

W. A. F. HAGBORG (Winnipeg)

Motion re International Standardization of Technical Words

In 1935 at our meeting in Amsterdam, WILLBRINK proposed standardization of terminology in plant pathology and published a list of definitions. A Committee on Technical Words, appointed by the American Phytopathological Society, reported in 1939 and a Terminology Committee of the Canadian Phytopathological Society reported in 1949. The Canadian Society adopted the report which recommended the introduction of international action at this Congress. Recently, the Plant Pathology Com-

mittee of the British Mycological Society has reported on terminology and published a list of definitions.—The difficulties inherent in attempts to obtain agreement have been dealt with fully in these reports, but the Canadian Phytopathological Society believe that international standardization is desirable and have instructed me to initiate discussion of it. I move that a committee on the international standardization of technical words in plant pathology be named by the executive committee of Section PHP with the understanding that the committee will report to the next International Botanical Congress.

Discussion

The President of the Section, E. C. STAKMAN, suggested that an interim committee should be

appointed to deal with this question and similar motions of internal sectional interest that might be raised during the following days of the Congress. The committee should act as a sort of clearing house between July 1950 and the next International Botanical Congress.

E. VAN SLOGTEREN supported this solution on the understanding that E. C. STAKMAN would join the committee proposed.

E. C. STAKMAN promised to do so and suggested that the rest of the committee should be composed of the acting officers of the Section, i.e. the vice-presidents present and the recorders. After some preliminary work done by himself, he intended to put the committee members to work, so that reports could be prepared and reported to the next Congress.

There were no objections from the Section to the formation of such an interim committee.

SESSION 7

July 18th, 2—6 p. m., Attendance: 70 members

Chairman: F. C. BAWDEN, Recorder: K. BJÖRLING

SUBJECT:

Virus-Serology and Transmission of Virus

MARION A. WATSON (Harpenden, Herts.)

The Behaviour of Persistent and Non-Persistent Aphid-Transmitted Viruses

Insect-transmitted plant viruses are grouped as "persistent" and "non-persistent." Vectors of persistent viruses remain infective for long periods; those of non-persistent viruses become non-infective within 1 hour of leaving the infected plants. Persistent viruses are transmitted by a variety of insects and probably in several different ways. Non-persistent viruses are transmitted only by aphids or coccids, and have characters in common which suggest that they are a fairly homogeneous group.

The most likely interpretation of the behaviour of aphid-transmitted, and some hopper-transmitted, persistent viruses is that the insects act as reservoirs, virus being passed through the gut wall into the blood, and ejaculated with the saliva. Their transmission may be affected by internal secretions of the vectors, or by localisation of the virus in the plant tissues, or both.

The non-persistent viruses were at one time believed to be transmitted merely by contamination of the aphid's mouthparts, but the specificity of the vectors and the way in which feeding conditions affect their efficiency, are difficult to explain on this hypothesis. It has

been suggested that their transmission is similar to that of aphid-transmitted persistent viruses, but is interfered with by inactivators, possibly trypsin, secreted by the feeding insects. This would account for the increased efficiency of the vectors caused by fasting before feeding on infected plants, and the decrease in infectivity with increased infection feeding time, which contrasts with the increase of infectivity shown by vectors of persistent viruses in the same conditions. The chief objection to this hypothesis is that infectivity can be acquired by a fasted aphid after only 30 seconds infection feeding, and transmission can be completed within 2 minutes, of which only 30 seconds may be actual feeding on the healthy plant. This short period seems to preclude the possibility of circulation through the body of the insect. Other alternatives are:—1) that the virus passes directly through the thin walls of the oesophagus into the salivary glands which lie on either side of it; 2) that either the stylet ducts, or the ducts and the oesophagus form the reservoir for the virus; 3) that the stylet ducts are emptied by the fasting period, and that virus containing sap runs up the salivary duct by capillary attraction and fills the salivary pump.

To assess the plausibility of these different hypotheses we need to know the rates of uptake of liquids by aphids in different feeding conditions, the capacity of the stylet ducts and associated parts, the plant tissues fed on at the critical times and the concentration of virus materials in these tissues. Feeding experiments using radio-active isotopes give some promise of resolving some of these problems.

K. SILBERSCHMIDT (São Paulo)

Experimental and Spontaneous Transmission of "Infectious Chlorosis" of Malvaceae

Within the general group of plant virus diseases, the "infectious Chlorosis" of *Malvaceae*

(= *Abutilon* mosaic) occupied for many years a very peculiar position, since diseases of this type seemed to be transmissible exclusively by grafting. These earlier findings, obtained with *Abutilon striatum* Dicks. var. *Thompsonii* Veitch in countries, where a natural spread of this disease had been never observed, left open the question of the natural dissemination of "Infectious Chlorosis" in other countries and brought into existence many theories about the possibility of a spontaneous generation of virus in plants.

In the neighbourhood of São Paulo, Brazil, and later on in many other regions of tropical and subtropical South America, I had the opportunity to observe the natural spread of a disease, very similar in its symptoms to those of "Infectious Chlorosis" of *Abutilon*, among *Malvaceae* (principally *Sida acuta* Burm. var. *carpinifolia* (L.) K. Schum. and *Sida rhombifolia* L.) which there belong to the common weeds of the open "camp" vegetation. This disease had been shown already by KUNKEL (1930) to resemble closely *Abutilon* mosaic in symptoms and behaviour. Before studying the way of natural dissemination of this disease I performed (1943) some series of grafting experiments, which showed that in the two species of *Sida* mentioned before, symptoms of "Infectious Chlorosis" could be induced by scions of *Abutilon striatum* Dicks. var. *spurius* Lynch., a species cultivated in gardens in São Paulo. From further grafting experiments I learned that the spontaneous "Infectious Chlorosis" of *Sida* which in its symptoms is indistinguishable from the disease induced in *Sida* by *Abutilon spurium*, could be easily transmitted from diseased to healthy plants within the species *Sida acuta* Burm. var. *carpinifolia* (L.) K. Schum., *Sida rhombifolia* L. and *Sida Glaziovii* K. Schum. Later on (still unpublished) I succeeded in transmitting the disease by the same method to *Sida micrantha* St. Hil., *Sida purpurascens* Salzm., *Malachra alceifolia* (L.) Presl. and *Abutilon Theophrasti* (= *Ab. Avicennae*, Gaertn.).

Starting in 1943 experiments on the manner

of the spontaneous spread of that disease, I had the benefit of the cooperation of Mr. ANTONIO ORLANDO, an entomologist of our Institute, during a great part of these studies.

After unsuccessful attempts with 20 species of insects and one species of mite, all of which collected from diseased *Sida* plants and considered possible vectors of "Infectious Chlorosis", we succeeded in transmitting this disease by a white fly (*Homoptera*, *Aleurodidae*), later on identified as being *Bemisia tabaci* (Genn.). In this earlier phase of our experiments (published in 1946) we could induce symptoms in 128 plants of *Sida rhombifolia* and 55 plants of *Abutilon striatum* by exposing them to viruliferous adults of the insect-vector *Bemisia tabaci*.

Taking up again these experiments in the current year (unpublished, 1950), I succeeded in transmitting the disease by the same vector not only to *Abutilon Theophrasti* but also to *Phenax Sonneratii* (Por.) Wedd., an *Urticacea*, which according to earlier observations of mine belongs to the natural hosts of this disease in the State of São Paulo.

Presently I try to compare the behaviour of the causal agent of our "Infectious Chlorosis" with that of the virus responsible for the disease displayed by *Abutilon striatum* var. *Thompsonii*. Although these experiments are still in progress, there seems to be no doubt that the general problem of the spontaneous dissemination of "Infectious Chlorosis" has ceased to be a puzzle.

K. STAPP (Braunschweig)

Über Stand und Bedeutung des serologischen Virusnachweises von Kartoffelviren in Deutschland

An Kartoffelmosaikviren kommen in Deutschland das X-, Y- und A-Virus vor. Für diese 3 Viren können entsprechende Antiseren hergestellt werden. Das jeweilige Antigen wird für X- und Y-Virus aus Preßsaft von vorher infizierten *Nicotiana tabacum*-Pflanzen, Sorte Samsun, das für A-Virus aus Saft der Sorte

White Burley auf chemischem Wege nach KAUSCHE und PFANKUCH gewonnen. Als Versuchstiere haben sich Kaninchen besser als Schafe und Ziegen bewährt. Die Antigeninjektion erfolgt ausschließlich intravenös. Das Antrocknen der Seren an Papier und der Nachweis mit der sog. "Blättchenmethode" hat den Vorzug äusserster Serumersparnis und bei X-Virus auch der grösseren Sicherheit. Der Prozentsatz der „unspezifischen“ Reaktionen ist nur noch gering und die Möglichkeit, auch in solchen Fällen zu klaren Ergebnissen zu kommen, besteht. Die serologische Nachweismethode ist für Wissenschaft und Praxis von grossem Wert. Für den X-Virus-Nachweis wird sie in ihrer Einfachheit, Schnelligkeit und Sicherheit von keiner anderen Methode übertroffen, vorausgesetzt dass bestimmte, näher zu erläuternde Bedingungen eingehalten werden. In wissenschaftlichen und praktischen Kartoffelzuchtbetrieben wird sie in Deutschland neuerdings bereits weitgehend angewandt. Auch zum Nachweis der Ausbreitung der X-Viren innerhalb ihrer Wirtspflanzen und zur Klärung anderer Fragen eignet sie sich vorzüglich. Quantitative Unterschiede lassen sich damit ebenfalls erfassen.

Der Y-Virus-Nachweis gelingt in infiziertem Tabaksaft immer, jedoch noch nicht mit derselben Sicherheit in der Kartoffelpflanze; das gleiche gilt in noch abgeschwächterem Masse für das A-Virus. Nach den jeweiligen Faktoren der notwendigen Sicherheitserhöhung wie beim X-Virus-Nachweis wird zur Zeit gefahndet.

Versuche, auch das gefährliche Blattrollvirus serologisch nachzuweisen, werden erst Erfolg haben, wenn es gelingt, ein entsprechendes stabiles Antigen zu gewinnen.

Discussion

B. EMILSSON: According to our experience based on a large number of parallel serological tests, juice inoculations on various test plants and stem grafts, the accuracy of the serological method of determining virus X is not 100 % but rather about 95 %.—The following ques-

tions may be raised: How was the accuracy of the method tested? Were pure strains or a mixture of strains used for injecting the rabbits? Is it possible to test plants sprayed with copper-containing compounds?

E. VAN SLOGTEREN: By working out a quick reaction (an agglutination-reaction) we were able to test 3000 samples per day. We got a sufficiently strong antiserum against virus Y to test it together with X by a polyvalent antiserum. 100 % security was proved by testing symptomless carriers. Plants sprayed with Bordeaux-mixture can be tested after washing them with water. Other points I hope to explain with the film at the end of the session.

J. G. BALD (Los Angeles, Calif.) *Development of Plant Viruses in Host Cells*

An attempt is made to outline a hypothesis that will rationalise our present limited knowledge of the association between a virus and the invaded cells of susceptible host plants. Viruses of the same general type as tobacco mosaic are considered. It is suggested that the particles of resistant viruses, e.g., tobacco mosaic, contain specific molecular configurations that are not exposed on the surface of the particles *in vitro*. The first stage of infection by a virus particle that has gained access into a cell includes a change in the particle that will expose these specific molecular configurations. It is further suggested that an infecting virus particle associates itself at a specific receptor site with constituents of the host protoplasm. This association may in some instances occur in plastid primordia. Allied with plant constituents the virus makes up a self-reproducing unit, similar to the minimum self-reproducing units postulated for normal cells. After the virus-plant units have produced more of their kind, virus may again be dissociated from the units and appear in recognisable form within the cell. At this stage the virus is no longer active in reproduction, but may be translocated to other

parts of the plant not already infected and again begin the cycle of multiplication.

Discussion

E. VAN SLOGTEREN: From serological agglutination-reactions we got the impression that the virus is exclusively or in any case mostly present in the plastids. We did not get any, or only a very weak precipitation reaction when the plastids were excluded.

K. SILBERSCHMIDT: May I draw the attention to the importance of the papers by M. WOODS and DU BUY for the theory of the importance of chloroplasts for virus multiplication.—Some experiments performed by me a few years ago on the multiplication of tobacco mosaic virus in detached tobacco leaves may be mentioned in this connection. On this occasion we inoculated the two halves of tobacco leaves with different concentrations of tobacco mosaic virus, and we found that even after 30 days there persisted a difference in virus concentration between the two halves of the tobacco leaves. This result seems to have some interest for the problem of virus multiplication.

L. M. BLACK: The electron micrography of tobacco mosaic virus in tissues of *Nicotiana tabacum* L. by BLACK, MORGAN and WYCKOFF shows an apparent association of the virus particles with chloroplasts. However, virus is present in the cytoplasm and so far these electron micrographs cannot be considered to have proved what the site of virus multiplication is in this case. The pictures do show an irregular distribution of virus and it may be that nutrients for virus are drawn from other cells. The cells first infected might then be expected to produce more virus than others before the nutrients become depleted. Something of this sort may explain the case mentioned by Dr. SILBERSCHMIDT.—Animal cells have mitochondria and I think Dr. BALD's hypothesis is probably intended to apply to them as well as to the plant plastids.

F. C. BAWDEN and L. M. BLACK continued the discussion.

HELEN PURDY BEALE and J. H. BEALE
(Yonkers, N. Y.)
A Virus Disease of Syringa vulgaris L.

A ringspot disease of *Syringa vulgaris* L. was observed in the vicinity of Yonkers, New York during the summer of 1949. The symptoms are similar to a virus disease of lilacs, occurring in North Bulgaria and described in an illustrated article by ATANASOFF in 1935 (ATANASOFF, D., Old and new virus diseases of trees and shrubs. *Phytopath. Zeitschr.* 8: 197-223, 1935.) Attempts to root cuttings from the affected shrub in September, succeeded in a single case. The following spring, the leaves on the lilac out-of-doors, and on the cutting in the greenhouse showed typical ringspot lesions or irregular bands of yellow tissue extending across the leaf blades. None of the premature defoliation occurred which, according to ATANASOFF, distinguishes the ringspot virus from the virus of lilac mosaic. It is believed that this is the first report of the occurrence of this malady in the U. S. A. Further investigation of the disease is being undertaken.

J. CALDWELL (Exeter)
Some Aspects of Seed Transmission of Virus

The general position of seed transmission of virus is reviewed and the fact stressed that seed transmission should correctly be considered as transmission of the virus in the seedling and not its presence in the testa or on the surface of the seed. It is argued that secondary infection of the embryo after formation is improbable if not impossible having regard to the fact that there is no protoplasmic connection between the nucellar tissue and the endosperm or between the endosperm tissues and the embryo proper. Primary infection of the megaspore or microspore mother cells is considered as unlikely in most plants especially tomato in the light of observations on the effects on meiosis of the virus of "Aspermy" disease of the tomato which has been under investigation for some years.

E. VAN SLOOTEREN

showed an interesting film of the new, well-equipped virus laboratory at Lisse.

SESSION 8

July 19th, 9-11 a. m., Attendance: 50 members

Chairman: K. STAPP, Recorder: K. BJÖRLING

SUBJECT:

Various Papers

G. GASSNER (Braunschweig)
Neuere Untersuchungen über die Flugbrandbekämpfung bei Weizen und Gerste

Die Warmwasserbeizung ist auch heute noch das allein wirksame Verfahren zur Bekämpfung von Weizen- und Gerstenflugbrand; jedoch gibt es keine Kombinationsmöglichkeiten von Temperatur und Einwirkungsdauer, die gänzlich ungefährlich für das Saatgut sind. Wirksame

Temperaturen bedingen stets auch schon gewisse Schädigungen der Keimkraft des Saatgutes, deren Höhe weitgehend auch von dem Zeitpunkt der Trocknung abhängt. Die Einschaltung einer 1- bis 2-tägigen Lagerung des geheizten Getreides vor der Trocknung bedingt bessere Keimprozentage und eine deutliche Beschleunigung des Keimverlaufes.

Während der Warmwasserbehandlung werden die Lebensvorgänge in den behandelten

Körnern stark aktiviert; da diese Aktivierung unter Sauerstoffabschluss erfolgt, müssen wir mit dem Auftreten schädlicher Nebenprodukte rechnen, die wohl, wie der künstliche Alkoholzusatz zur Beizflüssigkeit zeigt, die Beizwirkung auf den Pilz steigern, andererseits aber bei zu schneller Rücktrocknung nicht rechtzeitig abgebaut werden und schädliche Nachwirkungen auf das Korn verursachen. Die Einschaltung einer 1- bis 2-tägigen Lagerung zwischen Beizung und Trocknung gibt den behandelten Körnern offensichtlich die Möglichkeit aus der durch die Heisswasserbeize bedingten Aktivierung wieder in ein normales Stadium zurückzukehren und damit Schädwirkungen durch sofortige Trocknung zu vermeiden oder doch herabzusetzen.

Ein besonderer Übelstand der bisher zur Flugbrandbekämpfung verwendeten Tauchbeize besteht in der übergrossen Wasseraufnahme der gebeizten Körner; die Rücktrocknung des übermassen Saatgutes macht grosse technische Schwierigkeiten, auch sind die aufgeweichten Körner gegen mechanische Verletzungen besonders empfindlich, so dass weitere Keimschäden eintreten können. Die einzige Möglichkeit, die bisherigen Übelstände zu beseitigen, besteht in dem Übergang von der Tauchbeize zur *Warmbenetzungsbeize*. In meinen älteren Versuchen ist mit Flüssigkeitsmengen von 4 bis 12 l je 100 kg Saatgut gearbeitet; da die Beizwirkung beim Übergang von 10 l zu 12 l noch stark ansteigt, wurden neuerdings Flüssigkeitsmengen von 15 bis 20 l je 100 kg zur Anwendung gebracht. Dadurch wird die Beizung wesentlich zuverlässiger gestaltet als es bei den früher verwendeten Flüssigkeitsmengen bis zu 12 l/100 kg möglich war. Für die Bekämpfung des Gerstenflugbrandes empfiehlt sich eine Aufwandmenge von 17 bis 18 l je 100 kg und eine 3-stündige Beizung bei Temperaturen von 46° C, für die Bekämpfung des Weizenflugbrandes eine Aufwandmenge von 20 l je 100 kg und eine 3 1/2-stündige Beizung bei Temperaturen von 47 bis 48° C.

Die technische Durchführung der Warmbenetzungsbeize stellt kein ganz einfaches Pro-

blem dar; der Gebrauch rotierender Trommeln ist möglich, erfordert jedoch recht komplizierte und kostspielige Einrichtungen; einfacher ist es, das vorher entsprechend benetzte Getreide in lamellenartige Schächte von wenigen cm Querschnitt einzufüllen, deren metallische Wände von Wasser der erwähnten Beiztemperatur umspült werden. Das Getreide wird hierbei also während der Beizung nicht bewegt und nimmt durch einfache Wärmeleitung in weniger als 1 Stunde die gewünschte Beiztemperatur an. Nach der Beizung wird das Saatgut nicht abgeschreckt, sondern zum Abdampfen nur kurz ausgebreitet, wobei die Temperatur innerhalb weniger Minuten auf ungefährliche Werte absinkt.

Discussion

E. VAN SLOTEREN: Haben Sie auch Versuche gemacht, um die Wirkung der Vorbehandlung des Getreides zu studieren? Wir haben gefunden, dass die Vorbehandlung unserer Blumenzwiebeln sehr wichtig ist für die Resultate der Behandlung mit heissem Wasser oder mit heisser Luft.

G. GASSNER: Es ist schwer, Getreidekörner und Blumenzwiebeln zu vergleichen: 10–15 % Wassergehalt gegenüber etwa 80 %, ausserdem verschiedene Begriffe des Ruhezustandes. Aber auch bei Getreide ist der Zustand während der Beizung wichtig, insbesondere spielen die Ernte-verhältnisse eine grosse Rolle, indem die Empfindlichkeit des Saatgutes sehr verschieden sein kann.

A. J. P. OORT: 1) In Holland haben wir die Erfahrung gemacht, dass das Wetter vor und während der Ernte einen sehr grossen Einfluss auf die Resultate der Beizung hat. Eine Behandlungsdauer und Temperatur, die erfolgreich ist wenn das Getreide unter günstigen Umständen geerntet ist, kann mehr oder weniger erfolglos sein und Keimschädigung hervorrufen, wenn das Getreide unter ungünstigen Umständen geerntet ist. 2) Keimschädigung, hervorgerufen von der Beizung, kann zum Teil ausgeglichen werden durch eine mehrmonatige Trockenlagerung vor dem Aussäen.

G. GASSNER: 1) Den Ausführungen ist beizupflichten. Am besten lässt sich Saat beizen, die unter normalen Klimabedingungen geerntet ist. Ist das Erntewetter zu feucht gewesen, haben wir leicht zu hohe Keimsschäden; das Saatgut ist so empfindlich, dass man nicht immer die erforderlichen hohen Temperaturen anwenden kann, ohne dass sich starke Keimsschäden einstellen. Andererseits kommt es bei sehr trockenem Erntewetter leicht zu Verletzungen des Saatgutes beim Drusch; diese Verletzungen bedingen ebenfalls leicht höhere Keimsschäden. 2) Diese Beobachtungen lassen sich wohl mit den Ausführungen des Vortrages im Einklang bringen; es ist durchaus denkbar, dass lange Lagerung nach der Trocknung ähnlich günstig wirkt wie die Einschaltung einer wenig-tägigen Feuchtlagerung vor der Trocknung.

W. H. BURKHOLDER (Ithaca, N. Y.)

Certain Bacteria that Cause Rots in Tubers and Bulbs

Bacterial rots of onion bulbs in New York State are caused by *Pseudomonas cepacia* and *Ps. alliicola*. These species do not infect the growing plant but attack the bulbs when topped at harvest time. *Erwinia atroseptica* and *E. carotovora* while capable of rotting onions are seldom involved in such rots naturally. These two species of *Erwinia*, however, and various species of *Bacillus* are the common initiators of soft rots in potato tubers. *E. atroseptica*, the blackleg pathogen is isolated more frequently from tuber rots than is *E. carotovora*. *E. atroseptica* may be carried on the cutting knife when preparing potato tubers for planting, and results in seed piece decay in the soil or the blackleg disease of the plant. *E. carotovora* has not this ability. *E. atroseptica* may cause at 3° C a slow-spreading rot of the tuber that is black and moist. *E. carotovora* produces no rot at 3° C but causes a rot at 6° C or above that is frequently dry and buff colored. The black color is caused by the production of a melanin from tyrosine and is a reaction of the potato. Neither bacteria produce tyrosinase. Melanin is formed in a

neutral or alkaline medium and not produced under very acid conditions. Generally, *E. carotovora* produces more acid than *E. atroseptica* does which thus acts as a preventative in the production of the black pigment. *Bacillus subtilis* (*B. mesentericus*?), *B. polymyxa* and other species of this genus may cause a rot of potato tubers. These species have an optimum temperature of 35° C or above, which is approximately the maximum temperature for the *Erwinia* species. The conditions under which the *Bacillus* spp. cause rots occur at high temperatures as at digging time when injured tubers are exposed to the sun. Also, the high temperature storage of tubers in the potato chip industry is ideal for such rots. Pathogenic species of *Bacillus* may be isolated from apparently healthy tubers and infection may occur from either internal or external bacteria. The typical soft rot symptoms with foul odor, light colored foamy appearance and watery exudate arise after initial infection by the above pathogens, and are caused by secondary bacterial invaders. These saprophytic invaders are generally gas producers and are aerobes, anaerobes and microaerophiles. They usually reduce nitrates and are saccharolytic. The microaerophiles are weak starch hydrolysers. Cellulose decomposers have not been found. The secondary invaders or similar bacteria may be isolated from apparently healthy tubers.

Discussion

K. STAPP: Von 121 Kartoffelfäuleerregern, die von mir seinerzeit aus frischem Material aus verschiedenen Ländern isoliert worden waren, gehörten etwa 80 % zu *Bacterium phytophthorum* Appel, was sich serologisch einwandfrei nachweisen liess. Deshalb ist von mir vorgeschlagen worden, dass *B. phytophthorum* als Gruppenbezeichnung für die Kartoffel-Nassfäuleerreger gelten möge.—Die Bildung von Melanin bei der Zersetzung der Knolle hängt nach eigenen Untersuchungen mehr von der Kartoffelsorte als vom Nassfäule-Erreger ab.—Es ist eine grundsätzliche Frage, ob Sporenbildner, die Kartoffeln erst bei Temperaturen von

35°C angreifen, also einer Temperatur, die bereits auf das Gewebe der Knolle nachteilig wirkt, noch als Parasiten angesprochen werden dürfen.

E. VAN SLOTEREN: Our experience is that *Bacillus carotovorus* may cause a 100 % loss if the stock is forced too early in the season, or at a too high temperature. The other half of the same stock forced at a later time or at a lower temperature will stay healthy.

W. H. BURKHOLDER: The temperature range of *Erwinia carotovora* is 6°–36° C so it will infect at relatively high temperatures. The *Bacillus* spp. grow well up to 50° C and may cause rots at higher temperatures than *E. carotovora*. Have you isolated the pathogen and proved it to be *E. carotovora*? This species has never been isolated from soft rots of onions in U. S. The bacteria here are *Pseudomonas alliicola* and *Ps. cepacia*.

N. F. BUCHWALD: I understand that you use the name *Erwinia atroseptica* as a synonym of *E. phytophthora*, commonly used in Europe? Are you able to separate *E. atroseptica* from *E. carotovora*? And if so do you find *E. atroseptica* on other hosts than potatoes?

W. H. BURKHOLDER: *Erwinia atroseptica* may be separated from *E. carotovora* on its physiological reactions in culture and on pathogenicity tests. *E. atroseptica* may infect many hosts and has been found frequently on cucumbers and melons.

JOHN T. MIDDLETON (Riverside, Calif.)

Pythium Root Rot of Leguminosae

Several *Pythium* spp. cause root rots of certain legumes in the United States of America. The principal species concerned are *P. aphanidermatum*, *P. debaryanum*, *P. irregulare*, *P. oligandrum*, *P. splendens*, and *P. ultimum*. The severity of the root rot varies according to host, soil temperature, soil moisture, past legume planting, and fungus species.

Inoculations were made by placing the fungi, grown on a whole grain medium, in sterile soil in waterproof containers. Optimum soil mois-

ture was maintained by weighing filled containers and supplying requisite water. A protectant was applied to the legume seeds and they were then sown in such a way as to minimize damping-off and permit plant growth prior to the onset of root rot. Controlled soil temperatures were secured by placing the containers in water baths maintained respectively at 15°, 20°, 25°, 30°, and 35° C within an ordinary glasshouse. The extent of the root rot was determined about one month later by weighing the epigeal portion of the plants. Each of the following legumes were used in separate experiments: *Cicer arietinum*, *Melilotus indica*, two varieties of *Phaseolus lunatus*, three varieties of *P. vulgaris*, *Pisum sativum*, and *Vigna sinensis*.

All the legumes tested were susceptible in some measure to root rot caused by one or more of the *Pythium* spp. In general, root rot was more pronounced when the optimum temperature for vegetative growth of the pathogen was either below or above the optimum temperature for growth of the suspect, and least pronounced when the two optima were similar. Host susceptibility in descending order is: *Phaseolus lunatus*, *P. vulgaris*, *Pisum sativum*, *Vigna sinensis*, *Cicer arietinum*, and *Melilotus indica*. The pathogenicity of the *Pythium* spp. in descending order is: *P. aphanidermatum*, *P. splendens*, *P. ultimum*, *P. irregulare*, *P. debaryanum* and *P. oligandrum*.

Two types of root rotting mechanisms appeared to operate: one in which the fungus caused root rot only as conditions were less favorable for plant growth and more favorable for pathogen development; the other in which the fungus was able to cause some root rot at all temperatures employed. The most severe root rotting was of the first type, and frequently caused the plants to collapse within two weeks. Plants were not killed in the second type of rotting, and infection was evidenced by a slight reduction in plant weight, some leaf chlorosis, and root browning.

These results in part may indicate that LEACH's law for severity of pre-emergence

damping-off can be applied to root rot of seedlings or mature plants.

Although certain legumes are not materially affected by some *Pythium* spp. they nonetheless perpetuate the fungi in the soil and so contribute to root rot of a different succeeding legume crop. For example, root rot of *Phaseolus vulgaris*, caused primarily by *P. aphanidermatum*, is more severe following *Vigna sinensis* than following *Cicer arietinum*. Root rot of susceptible crops may often be lessened by adjusting the planting date to coincide with the optimum soil temperature for plant growth.

Discussion

N. T. FLENTJE: In Australia we have good evidence of *Pythium* spp. on many leguminous plants. With *Pisum sativum*, however, our main trouble is pre-emergence blight caused by *P. ultimum* and *P. debaryanum*. Even in soils heavily infested with these organisms, root rot of the growing crop does not appear to be serious. If in areas where pre-emergence blight of peas has been severe, pastures containing clover are sown, the clovers often fail to develop but appear to be attacked through the stems and roots by *Pythium*. These *Pythium* spp. have excellent powers of survival in dry soil. Soil stored air dry for a period of 6 months when subsequently wetted shows a profuse growth of *Pythium* mycelium, presumably from the rapid germination of oospores.

I. REICHERT: *Pythium* spp. in Israel seem to require a high temperature. Our *Citrus* seedbeds are affected firstly by *Rhizoctonia* but only later by *Pythium*. Besides we have a tomato root disease caused by *Pythium*.

LOUISE HEIMBECK: Root tips of peas are not spoiled by the *Pythium* hyphae unless filterable bacteria are present (i.e. contaminated seed). The filterable bacteria attack the meristem and stop growth. The hyphae of *Pythium* permeate the whole of the root cortex and the cap—facilitating the access of the filterable bacteria to the root meristems.

GERMAINE DEBRAUX (Poitiers) *Chimiothérapie du mildiou de la vigne par les composés organiques*

Il existait deux méthodes de culture du Mildiou de la Vigne en permanence au laboratoire: celle de STAUDERMANN, basée sur la culture de plants de Vigne en pots et la méthode des cultures associées de tissu cambial de Vigne et du *Plasmopara viticola* de MOREL. Une troisième, plus simple et moins onéreuse, repose sur la résistance remarquable et la longévité de la feuille de Vigne isolée conservée en survie. Une souche de Mildiou est entretenue au laboratoire depuis Juillet 1946 par pulvérisations hebdomadaires d'une suspension de conidies dans l'eau bidistillée. L'essai des substances anti-cryptogamiques est réalisé par pulvérisation sur la face inférieure des feuilles d'une solution ou d'une suspension du produit dans l'eau distillée à une concentration connue. Les feuilles sont abandonnées au séchage avant l'infection. 151 substances inorganiques, organiques et organométalliques ont été examinées par cette méthode. Le sel d'ammonium de l'hexanitrodiphénylamine ou aurantia s'est révélé comme étant la substance la plus active. Cette substance empêche le développement du Mildiou sur feuille de Vigne à la concentration de 0,000 025 Mol.g/L. soit 0,011 g. Il existe une assez grande marge entre cette concentration minima encore active et la concentration pour laquelle on observe des brûlures de la feuille (0,450 g par Litre). La valeur du seuil de toxicité de l'aurantia se rapproche de celle du sulfate de cuivre soit 1: 2 000 000. Cette substance provoque un retard accusé de l'expulsion des zoospores. On observe la production de zoospores plurivalentes provenant d'accidents du clivage cytoplasmique des conidies ainsi que la fusion entre zoospores se produisant immédiatement après leur émission. Il se produit de véritables plasmodes zoosporiens munis de plusieurs appareils flagellaires. Les propriétés de la couche limitante des zoospores sont modifiées, la cytolysse intervient rapidement ce qui évoque l'idée d'une perturbation de la permé-

abilité cellulaire. Une formule d'utilisation pratique de l'aurantia, reposant sur son adsorption par la caséine solubilisée par un alcali, la chaux, a été établie; le sulfate d'aluminium a été choisi pour neutraliser la bouillie, qui, sous l'action des eaux de pluie ou de rosée, libère progressivement l'aurantia à une concentration qui demeure suffisante pendant très longtemps. Les essais de la valeur préventive de la bouillie ont été réalisés en trois étapes: 1° sur feuilles isolées; 2° sur plants de Vigne en pots; 3° sur le terrain, par une méthode originale, au cours de l'été 1947 pendant lequel la température élevée et le degré hygrométrique très faible excluaient toute attaque d'épidémie de Mildiou dans la nature. Enfin, des essais de stabilité de la substance active à l'air et à la lumière ont montré que le produit considéré pouvait entrer dans une préparation anticryptogamique d'intérêt pratique.

MINA NADEL-SCHIFFMAN (Rehovot)

*Une contribution à la pathogénicité du
Penicillium digitatum et Penicillium italicum sur les fruits des Agrumes*

Cette communication traite des différences dans la pathogénicité de deux espèces de *Penicillium*, *P. digitatum* et *P. italicum* qui attaquent les fruits de différentes Agrumes: soit les fruits tombés par terre dans les orangeries, soit les fruits conservés dans des caisses.

Elle s'occupe aussi de l'influence des facteurs écologiques (température, humidité, qualité du sol) sur la quantité des fruits attaqués par ces deux espèces de *Penicillium*.

L'étude montre de même que le *Penicillium digitatum* est de nature plus parasitaire que le *Penicillium italicum*. Ce dernier est plutôt

secondaire et apparaît, dans la majorité des cas, sur les fruits déjà attaqués et désagrégés par d'autres champignons (par exemple le *Phytophthora*), tandis que *Penicillium digitatum* attaque le plus souvent les fruits, qui n'ont pas encore été atteints.

Ce travail montre en outre que l'infection par le *P. italicum* des fruits tombés à terre dans les orangeries commence du côté du fruit qui touche la terre, et que celle du *P. digitatum* atteint en premier lieu la partie du fruit qui n'est pas en contact avec la terre.

Discussion

G. VIENNOT-BOURGIN: Madame NADEL-SCHIFFMAN, en dehors des facteurs de développement qui distinguent ces 2 *Penicillium*, a-t-elle constaté un phénomène d'antagonisme entre ces 2 espèces?

A. CICCARONE: In Italy damages by *Penicillium* on fruits attached to the tree are put in relation with the environment conditions of the trees or of different branches of the same tree, with insects lodged at the base of the fruit under the calyx and with the health conditions of the tree ("Folge-" or "Kettenscheinungen" of FALCK). I would like to ask two questions. Has the infection been noticed on fruits still attached to the tree? If so, have there been apparent previous parasitic or non-parasitic damages?

MINA NADEL-SCHIFFMAN answered yes to the two last-mentioned questions.

L. J. KLOTZ: In California we find we can usually recover both species from naturally infected fruit even though one completely obscures the other. We also find that *Penicillium digitatum*, too, can act as a contact decay but much less vigorously than *P. italicum*.

SESSION 9

July 19th, 2—6 p. m., Attendance: 50 members

Chairman: E. C. STAKMAN, Recorder: K. BJÖRLING

SUBJECT:

1. *Factors Affecting Epiphytotic Diseases,*
2. *Report of the Committee on the Classification and Nomenclature of Plant Viruses*

E. VAN SLOGTEREN (Lisse) *Coming and Going of Plant Diseases*

The number of plant diseases has increased enormously since the last fifty years, partly as a normal consequence of the growing attention to the plant diseases; but often the alarming statements of plant doctors are based on the appearance of secondary parasites or scavengers in shipments of fruit or other vegetable products. These often give more friction between the plant doctors of different countries than do the real diseases. Many theories are given to explain the origin of new diseases, but it seems doubtful whether all those are really new indeed.

Too much one-sided attention is paid to the study of the parasites. All agriculture is artificial.

Large areas are planted with too dense a population of one variety, or one species of plants; crop rotation is neglected, and soil-fatigue arises, and exhausting cultivation reduces the fertility of the soil that cannot be restored by one-sided manuring with artificial manure.

Still the world cannot exist any more without mass-production of food crops and other crops that the world population, also artificially increased, needs.

International cooperation for the production and for the research must make mass-production possible without starvation or poverty of any nation.

The world certainly would be in less disharmony if not all nations tried to become self-supporting in agricultural production as well as

in industry, but if every country would instead produce the crops that suit best its natural conditions of climate and soil.

This certainly would considerably reduce the production costs of many world-food products, and international cooperation in the study and the control of plant diseases would be promoted.

The pooling of all knowledge about plant diseases would in this way automatically become a common interest of all nations.

The reporting of all parasites and plant diseases may be attained but it should not lead to an automatic exclusion of the plant products by plant-quarantine measures that never have given and never will give a definitive solution for any plant disease problems.

Often the origin of new plant diseases may be due to the way of cultivation that gives an opportunity to parasites, earlier present in moderate and unharmed amounts, to reach in great quantities a weak spot of the host that has been caused by conditions too artificial for the crop.

The study of the pathological anatomy of the plants can give an explanation for the spread of the yellow-disease of the hyacinths (*Erwinia hyacinthi*) by the change in the way of cultivation. The same may be the case with the sereh-disease of the sugar cane.

Findings in any culture based on a thorough study of the spread of a disease may be a great help for other crops and it seems most important to make the origin of new diseases a permanent subject of discussion among all phytopathologists.

Discussion

W. BROWN: How was it that black-stem rust was able to spread to wheat in Australia?

E. VAN SLOGTEREN: Uredospores on straw are capable of living for many months if the straw is kept dry; no doubt the rust got into Australia by that means.

E. C. STAKMAN, F. C. BAWDEN and E. VAN SLOGTEREN took part in the discussion that followed.

P. H. GREGORY (Harpenden, Herts.)

Factors Controlling Plant Disease Gradients

The study, in progress at Rothamsted, of disease gradients (decrease in incidence with increasing distance from source) is fundamental to the control of crop disease by isolation. In comparing gradients it is necessary to use a standard unit of distance (preferably the metre), to express incidence of infection in standard terms (after applying the multiple infection transformation when appropriate), and to allow for the dimensions of the source. Data for insect-borne virus diseases are fitted well by the linear regression of log intensity on distance.

Data for dry air-borne fungus spores and pollen indicate that the decrease with distance is due to two factors: (1) diffusion of the cloud by atmospheric turbulence; and (2) diminution of the cloud by deposition. Under standard sets of conditions the concentration of the cloud at various distance from the source can be computed from studies by meteorologists, but little is yet known about deposition on the ground or on vegetation. Deposition is now being studied experimentally in the open air and in a small wind tunnel. Preliminary work has attempted to elucidate the relation between the concentration of spores in the air and the number deposited on standard spore and pollen traps as used in plant pathology and for air-borne pollen. The greater efficiency of small trap surfaces has been demonstrated. This fact may lead to improvements in the technique of applying crop protective sprays and dusts.

MARY D. GLYNNE (Harpenden, Herts.)

*Factors Affecting the Incidence of Eyespot *Cercospora herpeticoides* Fr., on Cereals*

Spores splashed from infected stubble infect young plants on which more spores are produced. The fungus penetrates successive leaf sheaths until it reaches the straw base which it weakens causing "straggling" in light and lodging in heavy crops. The area lodged increases both with percent straws severely infected and with weight of straw.

Incidence of eyespot depends on the amount of inoculum initially present, the extent to which conditions favour spread of the fungus and its survival on the plant, and on the presence of susceptible hosts.

All varieties of wheat and barley tested are susceptible, oats much less and rye still less susceptible.

The degree to which eyespot incidence of wheat increases with the frequency of preceding wheat and barley crops has been measured during ten years on Rothamsted plots and in surveys in different parts of Britain. Data from the latter gave an average percent infection following different types of cropping. Deviation of the percent infected straws from the expected value (calculated from previous cropping) can be used to indicate the effect of other factors on the development of the disease. This method, supported other evidence that eyespot incidence is high after heavy spring rainfall and increases with increased earliness and density of sowing. A few grasses have been found infected by eyespot in nature and more have been artificially infected but the disease is seldom serious in the first wheat crop after grass.

Application of nitrogenous fertilisers produces opposing effects on the severity of eyespot at harvest, one effect predominating in the field, the other in pot experiments. The fungus grows better and survives longer in the more humid atmosphere of lush crops, but the extra tillers produced delay penetration of and reduce the severity of eyespot on the central straws.

Reduction in plant density gives each plant more food so that it produces more tillers and the plant bases dry out more rapidly in thinner crops, both effects reducing the severity of the disease. Over a wide range of seed rates uninoculated plants show little variation in grain yield but that of infected plants increases with decrease in seed rate.

Spraying with H_2SO_4 burns off outer infected leaves; when applied before the fungus has penetrated deeply, healthy central shoots remain which respond to fertilisers giving increased yield with less danger of lodging.

Discussion

A. J. P. OORT: In Holland we observed the same as has been observed recently in England. Crop rotation and date of sowing play a very important part in the occurrence of the disease. Now the curious thing is that the disease nearly disappeared during the last 10–12 years, severe cases not being observed so far as I know. One could think that we instructed our farmers so well that they did not sow wheat or barley too early any more or that they did not grow these crops in too narrow a crop rotation. This may be true for a part, but I think that the climate plays also an important role. Now we have only few informations about the disease during the war, but after the war the disease was not observed to any extent. This may be correlated to the continental climate which prevailed the last years.

MARY D. GLYNNE: In 1946 a survey of winter wheat crops in Holland showed less disease than could be accounted for by previous cropping; this was probably partly due to the extensive replacement of winter by spring wheat begun in 1939 which would reduce the amount of inoculum built up, and partly to the lower rate of sowing and wider spacing of rows in Holland than is general in Britain.—The danger of eyespot in Holland is likely to be much less than that in England because the proportion of arable land devoted to wheat and barley is much less so that rotations are longer.

R. HULL (Harpenden, Herts.)

Some Factors Affecting the Incidence of Yellows Virus in Sugar Beet in Great Britain

Sugar beet Yellows has caused serious losses in Great Britain over the last eight years, the most severe attacks occurring in 1945 and 1949. In 1949 almost 50 % of the sugar beet crop was infected by the end of August, and it is calculated that this resulted in a reduction of sugar yield of 19.6 %.

The persistence of the virus and ease of transmission by the main field vector, *Myzus persicae*, make it possible for the sugar beet crop, which is free from virus at first, to become completely infected within three to four months of germination. The numbers and movement of the vectors are greatly affected by weather during the winter and spring. *Myzus persicae* causes the earliest and most severe attacks of Yellows in the root crop when it overwinters on infected plants such as seed crops and clamped mangolds. Both are considered to be of importance in the disease cycle in Great Britain, whilst groundkeepers and volunteer plants from previous infected crops may also be a virus source from which alate aphids can pick up the virus, but they are not generally colonised by aphids. When the young root crop has been infested with viruliferous aphids a fresh generation of alatae are eventually produced which spread the disease rapidly.

It is considered that an essential step towards controlling the disease in Great Britain is to prevent it spreading from seed crops and from mangold clamps. Partial control has been obtained in seed crops by spraying stecklings in autumn with insecticides and by raising them under cover crops; but better results have been obtained by raising stecklings in virus and aphid free areas, and transporting them to the usual seed growing areas for planting out. This control method is being applied to more than 50 % of sugar beet seed in 1951. The remaining acreage of stecklings will be raised under cover crops or sprayed, or have both treatments ap-

plied, and any beds showing more than 10 % infection in October will be destroyed.

Surveys in spring have shown that considerable numbers of mangold clamps are unused even by May and that 30-45 % were infested with aphids in 1949. Large numbers of alatae of various species, including *Myzus persicae*, migrate from clamps and farmers are advised and encouraged to clear up clamps by the beginning of April. Methods of preventing aphid infestation in clamps are being investigated.

In most years cultural practices which encourage an early and rapid growth of the root crop tend to minimise virus infection, the most important factor being sowing date. Fields with high plant populations may contract less percentage infection than those with low, but no cultural practices are known which will protect a field from serious damage in years when the disease is severe. Experiments are in progress to determine the effect of systemic insecticides, and endeavours are being made to find resistant plants.

Discussion

E. KÖHLER: Is Virus Yellows seed-transmitted?

R. HULL: No.

N. F. BUCHWALD: 1) Do the beet growers not consider it a very expensive procedure to transport the beet stecklings the far distance from North England and even from Scotland to Eastern England, and are the stecklings not damaged during the transport? 2) Do you not consider it important to have a long distance between the fields with root crops and the fields with seed crops? 3) Do the farmers practise the system with raising the stecklings under cover crops? In Denmark Dr. H. P. HANSEN has had good results with raising the stecklings under barley as a cover crop.

R. HULL: 1) It is an expensive procedure, but costs can be reduced with experience. The risks involved in transporting stecklings are not so great as might be expected. It has been done satisfactorily on a commercial scale in Great

Britain over distances of 200 miles. The increase in yield from healthy stecklings more than compensates for the cost of producing and transporting the stecklings. 2) The very severe attacks on crops grown adjacent to seed crops can be avoided by separation, but this measure has little beneficial effect on the general course of the disease. Even at a considerable distance from seed crops enough primary infections are caused to result in secondary spread which has serious effects. 3) Yes, and the practice has been extended considerably this year. It is unusual to get virus infections higher than 20 % in crops grown in this way, but this is not considered an adequate degree of control.

I. REICHERT (Rehovot)

A Biogeographical Approach to Phytopathology

General methods

The biogeographical approach to a given flora or population of pathogens of a certain locality may be implemented by classifying every pathogen according to the four known plantgeographical aspects. Each pathogen is evaluated in accordance with each aspect and receives a specific designation.

These aspects are: (1) the floristic; (2) the ecological; (3) the historico-genetical; (4) the migratory, as follows:

(1) the floristic fixation of pathogens is best achieved by delimiting on maps the areas of occurrence of the plant disease in question, regardless of ecological considerations; this is termed the *Distributional Area*, and each pathogen, a *Component*.

(2) the ecological description is obtained by tracing the ecological tolerances of a pathogen and its host in the laboratory and the field, with regard to humidity, temperature, climate, soil and topography. The pattern of ecological range is termed the *Ecological Area* or *Natural Area*, and each pathogen, so considered, an *Ecological Type*.

(3) the historico-genetical aspect of each pathogen is seen by (a) fixing the ecological tolerances of the pathogens and by delimiting their natural areas and that of the hosts; (b) ascertaining the center of distribution of taxonomically related units (species & genera) of the pathogen and host; (c) observing the relative number of affected hosts; (d) observing the prevalence of affected perennials vs. affected annuals. Such an area of origination is termed an *Elementary Area*, and the pathogen involved an *Element*.

(4) Every pathogen which has a migratory route in common with others is termed a *Migrant* and the area through which they pass, a *Migratory Area* or *Migratory Track*.

As an example, two pathogens are characterized according to the system described above:

A. *Sclerotium bataticola* Taub. is (1) a tropical-mediterranean Component, (2) a macrothermic-hygrophyllic Type, (3) a palaeotropical Element, and (4) a palaeotropical Migrant.

B. *Puccinia glumarum* Eriks. & Henn. is (1) a semi-cosmopolitan Component, (2) a microthermic-hygrophyllic Type, (3) a boreal Element, and (4) a boreal Migrant.

Methods on Control

Control includes (1) treatment and (2) prevention:

(1) *Treatment* requires (a) that it has to be considered unnecessary where ecological conditions are unfavourable to the organism; (b) application of fungicides must coincide, not only with the ecological rhythm of the host, but also with that of the pathogen; (c) type of fungicide and dosage must be governed by climatic conditions; (d) antagonistic organisms must be looked for in Elementary Areas. (2) *Prevention* requires: (a) search for resistant plants in the Elementary Areas; (b) quarantine regulations in agreement with phytopatho-ecological principles; (c) internal quarantine should be governed by local topo-ecological conditions; (d) customs quarantine should provide conditions favourable for development of the disease in question.

T. H. THUNG (Wageningen)

Report of the Committee on the Classification and Nomenclature of Plant Viruses

On behalf of Dr. JAMES JOHNSON, Dr. THUNG presented the following report to the Phytopathological Section.

This committee was first organized by the Fifth Botanical Congress (Cambridge 1930). The members appointed were H. M. QUANJER (Netherlands) and JAMES JOHNSON (United States) who were empowered to increase the membership.

A tentative system of nomenclature which became known as the "numbering and lettering system" was presented before the Sixth Botanical Congress at Amsterdam in 1935. This system was adopted "in principle" by the Sixth Congress, and the committee requested to prepare a more complete proposal for further consideration by the Seventh Congress scheduled to meet in 1940. By 1939 a fairly comprehensive and complete prospectus had been prepared in mimeograph form, a copy of which is attached to this report. The event of the war period, the postponements of the Botanical Congress and the publication of individual systems of nomenclature for the viruses have tended to delay progress. Because of the challenging proposals for nomenclature it also seemed desirable to yield time for sufficient trials and the considered judgment of virologists on the relative merits of the systems advanced. The committee on virus nomenclature appointed by the American Phytopathological Society in 1938 reached a similar conclusion in 1949. A copy of their recommendation will no doubt be in your hands.

A summary of the proposals that have been made is published in "Tijdschrift over Plantenziekten 55: 128-137, 1949," together with a list of all relevant literature to date. A reprint of this article is presented herewith as a part of this report.

With due consideration to all factors that have contributed to the problems before your committee, it seems best not to submit any new recommendation to the Congress at this time.

It seems highly desirable however, that a committee should continue deliberation on the proposals that have been made with the purpose of reporting its conclusions to the Eighth International Botanical Congress.

If the Congress desired to continue a committee on virus classification and nomenclature it should consider membership personnel because of the age or the professional retirement of one or more of its present members.

Respectfully submitted,

Dr. C. W. BENNETT	Dr. L. O. KUNKEL
Dr. JEAN DUFRENOY	Dr. H. H. STOREY
Dr. JAMES JOHNSON	Dr. T. H. THUNG

In the afternoon of July 19th a special meeting was convened to discuss these matters. At this meeting were present: F. C. BAWDEN, T. BLENCOWE, Miss M. P. BRULIN OUBOTER, R. V. HARRIS, P. LIMASSET, K. M. SILBERSCHMIDT, E. VAN SLOGTEREN, T. H. THUNG, and Mrs. M. A. WATSON.

Mr. BAWDEN thought that the question of virus nomenclature could now safely be delegated to a committee of the International Microbiological Congress shortly to be set up for the purpose. Mr. HARRIS, however, was of the opinion that this committee would not be likely to be representative of the plant-pathologists' point of view, particularly regarding the non-

isolable viruses. He thought that the present committee should, retiring members having been replaced, continue its exploratory work on virus nomenclature and prepare a report for the 8th International Botanical Congress in Paris in 1954.

Obviously the committee could work in conjunction with that to be set up by the Microbiological Congress. The meeting were in general agreement with this view and it now further suggested and agreed, regarding a British representative on the committee, that if Dr. SAMUEL felt unable to continue his membership, the Council of the Association of Applied Biologists in London, as being most representative of plant-virus workers in Great-Britain, might be asked to nominate a successor to Dr. SAMUEL.

Mr. BAWDEN further suggested that regional representation should be maintained in the committee and that new members should be invited where former members are removed or retired as in the case of Australia, Germany and Italy.

A short report of this meeting will be sent to Dr. JOHNSON and Dr. JOHNSON will be asked to suggest other persons for the representations which are to be renewed. New members suggested for replacing or addition are: Prof. Dr. E. VAN SLOGTEREN, Dr. K. M. SILBERSCHMIDT, Dr. E. KÖHLER (Biologische Zentralanstalt, Celle, Hannover, Germany), Dr. P. LIMASSET.

SESSION 10

July 20th, 9 a.m. — noon, Attendance: 20 members

Chairman: E. C. STAKMAN, Recorder: K. BJÖRLING

SUBJECT:

The Epiphytic Disease on Zostera marina

NEIL E. STEVENS,¹ and HAZEL R. ELLIS
(Keuka Park, N. Y.)

Wasting and Recovery of Zostera Marina on the Atlantic Coast of the United States of America

Wasting of eelgrass (*Zostera marina*) is the most striking example on record of a plant

disease bringing about devastation of a species over an extensive range, in a short period of time. It struck the coast of North America with greatest force in 1931. By 1932 it was apparent that *Zostera marina* had been virtually exterminated.

A *Labyrinthula* organism seems always to be

¹ Deceased on June 26, 1949.

present in dying eelgrass and is thought to be the cause of its wasting.

Environmental factors concomitant with wasting of eelgrass are high sea water density and temperature.

Recovery of *Zostera* has been slow and irregular. There has been such marked increase recently that by 1949 certain areas may be said to have attained their former abundance. Certain species of shell-fish have increased with the return of eelgrass.

Some factors that affect recovery are: rate of reproduction by seeds under different temperatures, ability of seeds to germinate on sea bottoms of different physical character, interference of growth by commercial activities, and competing species. Although not yet demonstrated experimentally, doubtless disease resistance of some eelgrass varieties is playing a major part.

A. R. A. TAYLOR (Fredericton, N. B.)
Observations on the Distribution, Growth and Ecology of Zostera Marina L. in Eastern Canadian Waters

The range of *Zostera marina* L. in eastern Canadian waters extends from local occurrences in warm tidal pools on the Bay of Fundy coasts; around Nova Scotia; extensively in the warmer waters of the Gulf of St. Lawrence to the "north shore" of the St. Lawrence River and as far as the Strait of Belle Isle. It is reported from James Bay and the west coast of Hudson Bay. It is now reestablished in most areas occupied prior to its destruction by the "wasting disease". Although it has largely recovered, the disease symptoms are found widely and, although varying in extent and intensity through the growing season, are present generally enough to suggest that the disease has become epiphytotic in the *Zostera* population. Both *Labyrinthula* and *Ophiobolus halimius* Diehl et Mounce have been found in Canadian east coast waters.

Observations indicate that the main factors affecting distribution are: (1) suitable substrate for anchorage, (2) salt water, (3) satisfactory il-

lumination, (4) freedom from prolonged exposure to air, (5) shelter from the main violence of the open sea, and (6) an ice-free season of at least three to four months. The findings of OSTENFELD (1906), JOHNSON and YORK (1915), SETCHELL (1929) and TUTIN (1938) have been generally confirmed for our waters, although it appears that the temperature range over which *Zostera* flowers goes higher than stated by SETCHELL, but at higher temperatures few normal fruits are formed.

One major effect *Zostera* has on the habitat is to slow the movement of water amongst its plants, thus accelerating sedimentation and also decreasing the erosive action of waves and currents. The marine soil on which *Zostera* flourishes best in our area is a firm sandy mud, although it has been observed to grow on soft fine silt and coarse stony gravel.

In protected inlets densest growth of *Zostera* occurs at a depth of one to two feet at mean low water, close to the place where the plants occur nearest to the shore. Growth density decreases as depth and distance from shore increase; whereas size of plant as expressed by length and width of leaves, increases with depth towards the lower limit of occurrence.

If eel-grass plants are defoliated and the growing points removed, most rhizomes do not regenerate new upright shoots. Transplants of rhizomes were successful only when organized growing points were present.

It is suggested that studies of the biology or ecology of *Zostera* may help to suggest where some weakness might lie which would permit the sudden destruction of the members of this species on the occurrence of special environmental condition.

T. G. TUTIN (Leicester)
Some General Aspects of the Zostera Problem

The diminution in abundance of *Zostera marina* is one of the most striking events observed amongst plants, both in its speed and magnitude. Between 1930 and 1933 about 90 % of the plants on both sides of the N. Atlantic disap-

peared. This phenomenon may have been caused by pathogenic organisms, change in ecological conditions, some 'internal' change in the plant itself or by a combination of two or more factors.

Much effort has been spent on the search for pathogens and at least two have been found to be widespread. These two organisms, a protozoan and a fungus, both cause blackening of the leaves, followed by breaking off from the plant and may also cause injury to the rhizome. They can thus do serious harm and finally kill the host; but do they in fact account for the great reduction in its abundance? It seems unlikely that they first became parasitic on *Zostera* about 1930 over almost the whole of its range in the Atlantic, and if they had been living on it for years did they suddenly and more or less simultaneously become much more virulent? It seems to me that the explanation of the 'disease' is to be sought in a change either in the environment or in *Zostera* itself.

It has been suggested that a diminution in illumination on *Zostera* beds may have been a factor (TUTIN 1938), but arguments have been produced against this view (ATKINS 1938-9).

The difficulties of postulating an internal change in the plant are manifold but it is worth considering whether such a theory is tenable as it would seem to provide the best means of explaining the observed phenomena. The death of many kinds of plants after flowering is well-known; some flower and die within a year, others in two years and apparently a smaller number, of which perhaps the bamboos are the best known, exhibit a longer but more or less constant periodicity. Within the life of a single shoot ageing changes in the meristem causing alterations in the characteristics of organs produced by it are becoming well-known through the work of ASHEY and WANGERMAN among others. The disappearance of the scented form of *Mimulus moschatus* is perhaps best explained by assuming that it was a single mutant which reached the end of its life. *Zostera* flowers and seeds readily over most of its range and one would therefore expect a steady replacement of

old plants by new. It has been shown, however, that germination is low and the establishment of seedlings very difficult on a more or less mobile substratum subject to a greater or lesser degree of wave action. Further it is known that *Zostera* spreads widely by means of detached pieces of rhizome; its establishment in Greenland is almost certainly the result of such vegetative spread. It therefore seems possible that at least many of the plants in both the European and American populations were in 1930 'old' plants which suffered severely from the attacks of parasites as a consequence of their senescent condition. From such heavily infected plants an unusually high degree of parasitism of otherwise vigorous plants might follow, resulting in the phenomena observed in 1930-33. The nearly simultaneous diminution of *Zostera* on both sides of the Atlantic would on this hypothesis have to be regarded as a coincidence.

The hypothesis is supported by the recent report (DEXTER 1950) of the re-establishment of a large stand of *Zostera* in Goose Cove, Cape Ann, Massachusetts. Here the mouth of the cove was nearly closed by a road many years ago and exceptionally wave-free conditions resulted. In these conditions the establishment of seedlings appears to have occurred on a large scale, and an area of about 30 acres is now completely covered with *Zostera*. In contrast to this, in the more exposed habitats near Plymouth there has been only a slight improvement in the condition of the plant (WILSON 1949).

Discussion

P. DANGEARD: Sur la côte atlantique française on observe actuellement une renaissance des herbiers à *Zostera marina*. Cette renaissance est lente et elle n'a permis jusqu'ici qu'un rétablissement partiel contrairement à ce qui s'est passé, semble-t-il en Amérique où l'état antérieur a pu être rétabli dans certains cas.

ELSA KYLIN: *Zostera* started to disappear at the same time as *Codium* started to appear just as was the fact in Norway. The disappearance of one and appearance of the other do not

need to have any relations to each other. At about the same time as *Zostera* certain forms of *Ulva* started to disappear and reappear. This may be partly due to an increase of the percentage of salt in water as well as more sewage being brought out in the water. The reappearance of *Zostera* started when the water was more brackish. There is a variation of types in *Zostera* and it may prove useful to map out where *Zostera* just now exists and what the biotypes look like.

A. R. A. TAYLOR: Have you observed whether *Zostera* seeds were carried very far? It has been my experience that most seedlings occur in sandy bottom near groups of plants already present, but separate from them.

W. DIEHL: *Labyrinthula* was found in the Pacific Ocean in the presence of healthy *Zostera*. In the Pacific, *Zostera* was also healthy long after it was diseased in the Atlantic. Therefore the hypothetical ecological shock of the Atlantic region must not have affected the Pacific. There is a significant lack of evidence of etiology, provable by inoculations using pure cultures of host and suggested parasites.

R. B. STEVENS: Work is now being done, although to get support is difficult, on controlled inoculation experiments with *Labyrinthula*.

K. FAEGRI: The senescence theory as proposed by Prof. TUTIN cannot be strengthened by reference to plants belonging to other biological types (e.g. *Calluna* + a small tree—hapaxanth). The simultaneous dying out of *Zostera* within its enormous range of distribution is more in accordance with an explanation by reference to pathogenic agents and/or ecologic changes, than by reference to a very hypothetical senescence. Even if the hydrography of both sides of the Atlantic is rather different, the hydrographic circulation is but a part of the general atmospheric circulation which has changed very much during the last years.

J. A. STEVENSON: The question was raised as to whether other aquatics were involved during the time the *Zostera* "wasting disease" was under observation. During this time at one point in Chesapeake Bay it was noted that *Potamogeton* and other aquatics disappeared as did the *Zostera*. These plants returned after a few years.

PLANT PHYSIOLOGY, PHYS

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Recorder: H. LUNDEGÅRDH

Vice-Recorder: B. ÅBERG

SESSION 1

July 12th, 2—4 p. m.

Chairman: F. G. GREGORY

SUBJECT:

Absorption, Permeability and Transpiration

H. M. DIXON (Dublin)

An Experimental Demonstration of Sap Tension in Plants

Records of the movement of plant members during transpiration may be used to demonstrate the existence of tension in the sap. During transpiration these members are often flexed as the result of this tension. Following the fracture of the tensile stream, the straightening of such previously bent structures was recorded by photographic methods; this straightening was shown to take place with considerable rapidity.

*Discussion*¹

W. R. G. ATKINS: It is now nearly 46 years since first I had the privilege of hearing Professor DIXON's lecture on tension in sap and ever since when I have gone back to his laboratory I have been shown some interesting advance in the subject.

E. C. HUMPHRIES (Harpenden, Herts.)

The Absorption of Ions by Excised Root Systems

Barley plants were grown for about 6 weeks in water culture containing complete nutrients

or deficient in either nitrogen, phosphorus or potassium, and their carbohydrate content varied by use of shade. Two levels of deficiency of each element were employed. The excised roots of these plants were placed in a continuously flowing, aerated complete culture solution and their nitrogen, phosphorus and potassium content estimated after intervals of 2, 4, 8, 16 and 24 hours. The carbohydrate content (sucrose and reducing sugars) of the roots was measured on an initial sample and after 16 hours. The changes in respiration rate during treatment were followed on certain samples.

In the deficient samples, there was uptake of the element in which they were deficient, while usually in the samples grown in complete nutrient there was a loss of ions. Shading decreased the rate of uptake of the deficient ion. Carbohydrate content decreased with time in all samples and the respiration rate also decreased except when nitrogen (as nitrate) was being absorbed when it increased. This effect was due to synthesis of higher nitrogen compounds from nitrate. There was always a progressive decrease in the dry matter

¹ In all discussions only such remarks have been included, which were written down and handed over to the Recorder. Questions have been excluded in cases where the proper answer is lacking.

content of the excised roots during treatment, but in some cases an increase in fresh weight occurred due to an uptake of water. The data have been analysed to discover the factors determining loss or gain of ions. The progress curves for loss or gain of a particular ion may be represented by second-order equations and the rates, for a given ion, at 0 hours and 16 hours calculated. The relation between these rates and the ion and carbohydrate contents on the two occasions was investigated.

The results of the potassium experiment have been analysed. It is shown that ion and carbohydrate concentrations are, in general, the chief factors determining uptake or loss of a particular ion, whether at 0 hours or 16 hours, although in some cases certain other factors appear also to be concerned.

It is also shown that uptake or loss of water by the excised roots is connected with carbohydrate content.

Discussion

K. V. THIMANN: What is the nature of the material which is lost from the roots?

E. C. HUMPHRIES: We do not know. The material lost is not nitrate although it contains nitrogen. It must be some higher form of nitrogen.

W. A. ALBRECHT: In the case of the increased respiration (CO_2 output) when nitrogen uptake occurred, do you have any suggestion as to whether that extra CO_2 output was the result of increased catabolism of organic compounds or due to anabolic processes synthesizing the nitrogen into new compounds as parts of the plant, possibly proteins?

E. C. HUMPHRIES: The evidence of protein formation has been obtained in a subsidiary experiment, when nitrate was being absorbed.

K. HÖFLER (Wien)

New Facts on Water Permeability

In the Vienna Institute the influence of physical and chemical factors on water perme-

ability (w.p.) has been thoroughly investigated by F. SEEMANN. It is measured by the rate of plasmolysis and deplasmolysis. (HUBER and HÖFLER, 1930.)

Among the physical factors a rise in temperature increases the w.p. As found by BIEBL also an irradiation by ultra-violet rays causes an increase of the w.p. Both effects, however, are essentially dissimilar. The w.p. proves to be thermostable after heating without any aftereffects of previous temperatures being observed, whereas the increased w.p. after a short irradiation remains increased for many hours and finally vanishes after about 24 hours if the effect of the irradiation was reversible. As stated by BIEBL this increase of the w.p. may be followed by a decrease, so to say as a reaction.

Further studies were made by SEEMANN on the effects of salts and non-electrolytes. The w.p. of the cells when exposed to hypotonic and not yet plasmolyzing solutions and then measured by the rate of plasmolysis and deplasmolysis was increased by salts and decreased by non-electrolytes. In the first case the water-ways appeared to be extended, in the latter case they were narrowed.

As to narcotics a preparatory treatment by small quantities leads to a decrease of the w.p., whereas a higher concentration has the contrary effect. Small quantities of narcotics may liquefy the plasm lipoids and thereby reduce the water-ways.

As to the effect of pH, curves with a single peak were found, but BRAUNER thought this peak to lie around the IEP (pH 5.3). SEEMANN, who arranged the values more densely, arrived at a peak around 6-7 pH in the neutral zone.

Thus, physical factors have a strong influence on the w.p. The question is whether the plasm surface layers or the mesoplasm may be considered responsible for the resistance to the water passage. In our opinion there is no reason why the old dogma, which limits the permeability resistance to the boundary layers, should be extended to the penetration of

water too. Contrary to this it is suggested that the mesoplasm is most largely responsible for the resistance to the water penetration.

Therefore, conclusions may be drawn from the w.p. and its changes to the respective sub-microscopic protoplasmatic state.

Discussion

J. LEVITT: The increased permeability to water during deplasmolysis is no evidence for the role of mesoplasm in permeability. It can be explained as due to a rapid stretch of the plasma membrane, the lipids becoming separated. It is also possible to show that surface layer changes do occur during plasmolysis and deplasmolysis by macro-manipulation methods using oil drops as demonstrated by SIMINOVITCH.

K. HÖFLER: While I would rather like to see the increased water permeability during deplasmolysis to be alone an evidence for the role of mesoplasm, I have also given other arguments. Nevertheless I have often seen that the water permeability during deplasmolysis is increased rapidly in protoplasts showing a strong "systrophe"—the cytoplasm being contracted around the nucleus and therefore the layers of the mesoplasm having become very thin elsewhere. But I concede that further experiments are necessary to clarify that.

H. BURSTRÖM: I do not quite understand the reason why you cannot assume a change in the properties of the cytoplasm surfaces as causing changes in permeability, but only changes within the mesoplasm.

K. HÖFLER: As I have shown, the resistance of the plasm against penetration of water is chiefly offered by the mesoplasm and not by the surface layers. Thus, if the degree of water permeability is limited by the mesoplasm then the changes in water permeability will also have to be assumed as being caused by changes in the mesoplasm.—According to my experiences I must point out that the greatest changes of the surface layers, namely the disturbance of the plasmalemma by

plasmolysis, usually do not cause a strong change in permeability—whereas visible changes of the mesoplasm, e.g. swelling by salts, actually lead to a measurable change of water permeability.

L. BRAUNER: The relation between IEP and water permeability points to a dual mechanism of the control of the water diffusion. This fact is borne out by the opposite effect of pH-changes during plasmolysis and deplasmolysis.

K. HÖFLER: We did not yet feel compelled to assume a dual mechanism since SEEMANN obtained curves with a single peak at pH 6–7 during plasmolysis and also during deplasmolysis. It seems to me to be the chief thing that your curves of water permeability with a single peak were confirmed. The maximum of SEEMANN's curves seems somewhat shifted to the neutral zone. A theoretical explanation for that has not yet been attempted by us.

H. E. BREWER: Because of the much greater volume of the mesoplasm as compared to the plasma layers, how can you be sure that the greater resistance which you find in the mesoplasm is not merely quantitative rather than qualitative?

K. HÖFLER: You are right. It is sufficient to assume that the mesoplasm and the surface layers are equally resistant if reduced to the same thickness. I do not contend that the specific resistance of the mesoplasm is greater than that of the surface layers.

G. HYGEN (Oslo)

Experiments with Excised Objects in the Study of Plant Transpiration

In the majority of previous experiments with excised objects by the torsion balance method, the water loss has been measured during the first few minutes after abscission only, and the values obtained have been employed as estimates of the transpiration rate prevailing immediately before abscission. It is possible to obtain more information by this type of experiment when the transpiration decline in cut objects lacking water replenishment is followed during several hours.

The following procedure has been found to give consistent and reproducible results in experiments with more than 20 species of different ecological character:

1) The plant material is given a suitable pretreatment in order to induce maximum turgor and fully open stomata at the start of the experiment.

2) Constant external conditions are maintained throughout the experiment.

3) Fresh-weight determinations are made in short intervals during a period of several hours by means of a torsion balance.

4) By mathematical analysis of the resulting transpiration decline curve, the separate influence of increasing water deficit and stomatal closing upon the rate of water loss can be demonstrated.

5) Finally, three characteristic parameters are derived from each curve, estimating

a) the transpiration rate by maximum turgor and fully open stomata under the given conditions,

b) the transpiration rate by maximum turgor and completely closed stomata, and

c) the rapidity of the closing reaction.

This transpiration curve method can be

adapted to investigations in two main directions. In experiments with structurally different plants, performed under standard external conditions, a quantitative characterization of the individual transpiring properties of the objects can be obtained. In this way, statistically significant differences can be documented even between different populations of the same species. On the other hand, the physical problems of transpiration can be explored by variation of the external factors in experiments with homogeneous plant material.

Discussion

O. V. S. HEATH: I should like to ask Dr. HYGEN if he has never found any evidence in his experiments that the stomata open during the early stages of rapid wilting. It has been found by many workers from DARWIN (1898) onwards that the stomata at first open very widely and only later close when the leaf is wilted.

G. HYGEN: My experiments were not performed under conditions which would provoke rapid wilting, so for this reason I have not observed the effect referred to.

SESSION 2

July 14th, 9—11 a. m.

Chairman: E. K. GABRIELSEN

SUBJECT:

Photosynthesis

M. S. NISHIMURA, C. P. WITTINGHAM and R. EMERSON (Urbana, Ill.)

The Quantum Requirement of Photosynthesis

The quantum requirement of photosynthesis (minimum number of quanta absorbed by the plant per molecule of oxygen produced) has generally been found to be not less than about 8 or 10. For red light, this represents an ef-

iciency of about 25 per cent. Recently, WARBURG, BUREK, and co-workers have reported quantum requirements of about 3 to 5. If these exceptionally low quantum requirements represented the conversion of carbon dioxide and water to carbohydrate and oxygen, the indicated efficiency would be 70 to 80 per cent. It is possible that in these cases, oxygen production represents synthesis of carbohydrates not from carbon dioxide and water, but from

partially reduced intermediates of respiration. If this were the case, the very low quantum requirements would not represent such a high efficiency of energy conversion. It may later be necessary to explore this possibility, but we prefer to inquire first whether the photosynthesis measurements of WARBURG and BURK really indicate the rates of oxygen production which they claim.

They measured photosynthesis by a two-vessel technique which requires that the observed pairs of pressure changes in the two vessels represent exactly the same gas exchange. Small differences in the gas exchange represented by pairs of pressure changes can lead to large errors in the computed rate of photosynthesis, and hence in the calculated quantum requirement.

EMERSON and LEWIS have explained that extra carbon dioxide exchange is particularly likely to lead to differences in the gas exchange represented by pairs of pressure measurements. WARBURG and BURK believe that no extra carbon dioxide exchange was involved in their measurements, but we find evidence from their published data that extra carbon dioxide exchange was taking place during their measurements.

The vessel shapes which they used for the pairs of pressure measurements might be expected to increase the risk of inequality of gas exchange, because the circulation of the liquid cell suspension was not alike in the two vessels. Another important potential source of error was their choice of time intervals for measuring photosynthesis. They used short periods of exposure to their source of measured light, alternated with short dark periods (or periods of exposure to unmeasured compensating light). They allowed no time interval for the manometers to respond to changes in rate of pressure change following changes in illumination. They say that they saw no evidence of physical lag in the response of their manometers. We find in their data clear evidence of physical lag. We have used vessels closely resembling theirs in size and shape,

and have demonstrated not only physical lag, but different lag in the two members of the pair. Under these circumstances, large errors are to be expected from two-vessel measurements covering short intervals of light and darkness, because the pairs of observed pressure change do not represent the same gas exchange.

If we repeat their schedule of measurements, we can obtain data in confirmation of the pressure changes which they report. However, we do not believe these pressure changes represent the rates of oxygen production claimed by WARBURG and BURK. We find that if a suitable time interval is allowed after each change in illumination, to permit the two vessels to come to steady rates of gas exchange, so that corresponding readings represent equal gas exchange, then the pairs of pressure changes lead to calculated rates of oxygen production which represent quantum requirements of about 8 or 10.

The very low quantum requirements reported by WARBURG and BURK are based upon measurements which, when we repeat them, show clear evidence that the pressure changes in the two vessels do not represent the same gas exchange.

In our opinion, their measurements represent neither the rates of oxygen exchange nor the quantum requirements which they claim, and there is therefore no need to seek explanations for the exceptionally low quantum requirements in terms of oxygen production from intermediates of respiration.

The paper was read by R. EMERSON.

Discussion

A. W. GALSTON: 1. Is the situation regarding quantum yield measurements altered by the use of a compensating white light, as in the recent WARBURG-BURK experiments? 2. What is your opinion of the validity of the statement made by WARBURG-BURK that algae maintained at high pH values are moribund and therefore not operating at maximal efficiencies?

R. EMERSON: 1. No, the use of compensating white light does not eliminate extra carbon dioxide exchange brought about by turning on and off the red (measured) light used for determination of quantum requirement. An increment or decrement of light will bring about extra carbon dioxide exchange, even when there is continuous illumination with compensating white light. 2. We have seen no evidence that the steady-state rate of photosynthesis is appreciably lower in carbonate buffer at pH 9 than in phosphate culture medium at pH 5. Efficiency does not seem to be dependent on pH over this range.

C. S. FRENCH and VIOLET M. KOSKI
(Stanford, Calif.)

The Fluorescence Spectra and Photochemical Activity of Chloroplast Pigments

Measurements of the intensity of fluorescence emitted by the separate pigments in living material should permit estimations of the relative amounts of energy which the pigments may be receiving either by their own direct absorption of light or by energy transfer from their absorbing pigments. In order to determine by fluorescence whether or not energy transfer from one chloroplast pigment to another can take place as a step in photosynthesis it is necessary to make sure that the following effects do not introduce large errors: The change in fluorescence intensity with time and the lack of proportionality of fluorescence intensity to the incident intensity; the internal screening by inactive pigments; the influence of the varying depth of penetration of various incident wave lengths upon the reabsorption of the fluorescent light; the possible change in the quantum yield of fluorescence of a single pigment at widely separated wave lengths. Experiments are in progress to evaluate these effects in various species of algae and leaves. It has been found that in brown algae the reabsorption of fluorescent light is much greater with green than with blue incident light and this reabsorption may shift the

position of the main chlorophyll band by 6 m μ .

In red algae the fluorescence of phycoerythrin, 580 m μ , and of phycocyanin, 655 m μ , is constant with time while the 685 chlorophyll peak may vary greatly in brilliance under constant external conditions. These changes of brilliance with time are greatly influenced by the wave length and intensity of the incident light and by the state of the algae. The fluorescence spectrum of pure phycoerythrin has been studied in collaboration with Professor LAWRENCE R. BLINKS. Its fluorescence bands are in the same position in water solution and in the live algae.

The shape of the fluorescence spectrum of chlorophyll is very different, due to reabsorption, in leaves with a high concentration of chlorophyll and in leaves with a very low chlorophyll content.

An installation of two large grating monochromators with a high intensity mercury lamp, a tungsten bar lamp, and a photomultiplier tube with amplifiers, correction devices, and a recording potentiometer was used in these measurements. This equipment is capable of plotting automatically, on a linear wave-length scale, the fluorescence spectrum of samples which may be excited by various wave lengths of measured intensity in the visible region. It will also plot the visible absorption spectra of liquid samples applying all necessary corrections with an accuracy of about 1%. The monochromators may be used either singly or as a double instrument for irradiation of plants with narrow wave-length bands in the determination of action spectra.

The paper was read by C. S. FRENCH.

Discussion

J. H. C. SMITH: Was the intensity of chlorophyll fluorescence less on an absolute base at higher intensities than at lower intensities?

C. S. FRENCH: I think they are, but further calculations are necessary to determine this.

B. KOK: Is it possible that the very short time of measurement used by you is responsible for the inconsistency of chlorophyll fluorescence? Or was a pre-illumination given to reach a steady state?

C. S. FRENCH: In all the curves a pre-illumination period of several minutes was used and the constancy of the fluorescence at 685 $m\mu$ was established before recording the curves, which was then done without interrupting the illumination.

R. L. WEINTRAUB: If one observes a living etiolated cereal leaf with a spectroscope, the proto-chlorophyll absorption band can easily be seen at 620–630 $m\mu$. After several seconds of illumination this band becomes weaker and the chlorophyll band at $\sim 665 m\mu$ appears. How do you interpret this observation, which is, of course, a very old one, in relation to the action spectrum for chlorophyll formation with a maximum at $\sim 650 m\mu$?

J. H. C. SMITH: It is difficult to conceive of the absorption of proto-chlorophyll in the leaf as being at 620 $m\mu$, because the absorption in ether solution is at longer wave lengths ($\sim 624 m\mu$).

E. C. WASSINK: I should like to ask whether the objects are exposed under suitable conditions for photosynthesis?

C. S. FRENCH: The algae were lightly pressed against the front surface of a glass cell by a plug of glass wool. The conditions are not ideal but for a thin alga might allow a limited amount of photosynthesis to take place due to dissolved CO_2 in the sea water.

H. TAMURA: If I remember correctly, Dr. KAUSKY has once noticed that the fluorescence of living leaves shows, at the very beginning of illumination, somewhat different colour (longer wave-length) compared with that observed at later stages. Have you not observed such a phenomenon?

C. S. FRENCH: I had overlooked this report in the literature and am most grateful for having it called to my attention. We have not as yet observed this phenomenon ourselves.

H. TAMURA (Tokyo)

New Observations on Photosynthesis in Flashing Light

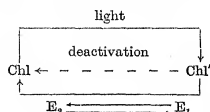
The study of photosynthetic phenomena under the condition of intermittent illumination is already known as one of the effective avenues of approach to the elucidation of photosynthetic mechanism. As it has been shown by EMERSON and ARNOLD in 1932, the photosynthetic yield per one flash is a function of carbon dioxide concentration, intensity of flashing light and the length of the dark interval between the flashes applied. By increasing these three factors sufficiently, these authors believe to have attained to the "maximum" possible value of the photosynthetic yield per flash, which was reported to be about 2000–3000 times smaller than the chlorophyll content of plant cells. This value was claimed to be quite temperature-independent, while the dark interval necessary and sufficient to bring about that "maximum" yield was shown to be largely temperature-dependent. Based on these data it has generally been believed that the photochemical intermediate built by each flashing light must be a fairly stable compound, and that the dark reaction which follows or precedes the photic reaction is temperature-dependent, being completed within about 0.01 sec. at 25°C and about 0.2 sec. at 1°C. The observation that the value of allegedly "maximum" yield per flash was strikingly smaller than the chlorophyll concentration gave rise to the so-called theory of photosynthetic unit, which once had held sway among the theories of photosynthetic mechanism.

Suspecting the validity of EMERSON and ARNOLD's data for several reasons, we repeated the same experiments using *Chlorella ellipsoidea* as plant material. The intermittent illumination was effected by cutting the light beam from an incandescent lamp with a rotating disc having symmetrical openings of appropriate widths at appropriate distance. By this arrangement we could produce flashing lights

having energies of as much as 988 luxsec., an intensity which can hardly be possible by the neonlamp as was used by the American authors.

By varying the dark interval in the range between 0.0073 and 0.600 sec., and the flash energy in the range between 12 and 988 luxsec., it was confirmed that the maximum yield per flash (under the condition of CO_2 saturation) to be obtained with sufficiently high flash energy and sufficiently long dark interval varies appreciably with temperature, viz., at 25°C 7.3×10^{-8} , at 15°C 5.3×10^{-8} and at 7°C 3.7×10^{-8} mole/gm. of dry weight of algae. These figures are decidedly larger than 1.15×10^{-8} mole/gm. (at $1^\circ\text{--}25^\circ\text{C}$) reported by EMERSON et al. Larger values, compared with those given by American authors, were also obtained for the length of the dark interval required to produce the maximum yield, namely 0.2 sec. at 25°C , 0.3 sec. at 15°C and about 0.4 or more sec. at 7°C . The gross discrepancy in these findings was shown to be due to the fact that the flashing lights used by the American authors were by far too weak to be able to produce real maximum yield.

The fact that the maximum photosynthetic yield per flash varies with temperature is difficult to explain except on the assumption that in the mechanism of photosynthesis there occurs a deactivation or back reaction of some photochemical intermediate. The nature of this unstable intermediate cannot concretely be ascertained by kinetic studies such as reported here, but it is tempting and also natural to assume that it may be some photoactivated state of chlorophyll. Tentatively, as perhaps the simplest possible kinetic schema of photosynthetic mechanism (under the condition of CO_2 saturation), we pictured the following cyclic reactions and investigated in what manner the deactivation of the photochemical intermediate would occur:



where Chl' means the photoactivated form of chlorophyll molecule, and E_1 and E_2 the certain catalytic factor in the BLACKMAN system before and after reaction with Chl' . The entrance of CO_2 and H_2O into, as well as the evolution of O_2 and $[\text{CHOH}]$ from, the reaction system, which are not considered in this schema, may happen by more or less complicated procedures, somewhere in the sequence of the reactions. Based on this schema a number of theoretical formulae expressing various phenomena to be observed in continuous as well as in flashing light were deduced. By checking these deductions with experimental facts, we came to the conclusion that the deactivation of the photoactivated intermediate does not proceed in a manner of first order reaction, but in a manner of a reaction of higher, probably second, order.

At any rate, our observations may be regarded as a decisive evidence against the theory of photosynthetic unit, according to which the maximum yield per flash represents the concentration of the "unit," therefore, a value which must be independent of temperature. According to our interpretation, this value represents a rather complicated term including not only the total concentration of Chl and E , but also various velocity constants assigned to the reactions assumed in the schema. Relevant revision must also be made to the prevailing concept that the length of the dark interval required to produce the maximum yield (0.01 sec. at 25°C according to EMERSON et al.) represents the reaction time of the BLACKMAN reaction, since the time period in question is dependent not only on the velocity of the reactions $\text{Chl}' + E_1 \rightarrow \text{Chl} + E_2$ and $E_2 \rightarrow E_1$, but also on the rate of the deactivation reaction $\text{Chl}' + \text{Chl}' \rightarrow 2\text{Chl}$, which is unfruitful for the accomplishment of the photosynthetic process.

In postulating a deactivation reaction of some photochemical intermediate, our concept has the essential point in common with that of FRANCK and HERZFELD who assume a back reaction of a photochemically activated

complex involving chlorophyll and a certain organic substance derived from CO_2 . According to these authors, however, the maximum yield per flash is interpreted as representing the concentration of the so-called Catalyst B which should act as a catalyzer to stabilize the unstable photochemical intermediate in question. Insofar as the concentration of this imaginary catalyst cannot be supposed to vary with temperature, their theory also is hardly reconcilable with the fact we have established.

It should be noted that the deactivation of photochemical intermediate, which we had tentatively assumed to occur in activated chlorophyll molecule, may possibly take place in some substance other than chlorophyll. Of great interest in this connection is the fact recently established by CALVIN and DOROUGH (1948) that the chlorophyll (b component) shows a phenomenon of phosphorescence in the infra-red region (at about 8600 \AA) with a life time of 0.03 second. It remains to be seen whether or not this phenomenon may have any essential bearing upon the observations and deductions we have made in the present work.

The experimental part of this work was done under the collaboration of Mr. Y. CHIBA.

Discussion

R. EMERSON: It is suggested that the difference in behavior of photosynthesis observed by Professor TAMIYA, compared to the observations of GAFFRON and RIEKE, and EMERSON and ARNOLD, may be due to the greater duration of TAMIYA's light flashes (about 100 times as long as those used by EMERSON and ARNOLD).

H. TAMIYA: The duration of flashes used by GAFFRON and RIEKE, and PRATT and TRELEASE was $4-5 \times 10^{-3}$ sec., while ours was between 6×10^{-4} to 8×10^{-3} sec. In their first report, EMERSON and ARNOLD had estimated their flash duration to be 10^{-5} sec. In their later report, however, they described it to be

4×10^{-4} sec., and with this duration they have obtained similar results as with flashes with much shorter duration. In a preliminary experiment we have confirmed that, when the flash energy is kept constant, the variation of the flash duration in the range between 6×10^{-4} and 6×10^{-3} sec. causes no serious difference in the yield, provided that the dark interval is sufficiently long compared with the flash duration. The necessary condition for the flashing light experiments, I believe, is the smallness of the ratio (flash duration)/(dark interval), rather than the absolute value of the flash duration.

C. S. FRENCH: Do the different species used show any difference in the dark recovery period?

H. TAMIYA: I do not know; so far, the experiments were carried out only with *Chlorella ellipsoidea*.

J. H. C. SMITH: Was there any difference in the length of dark period to achieve maximum photosynthetic yield when different concentrations of CO_2 were used?

H. TAMIYA: I have attempted to make that point clear, but did not succeed in getting accurate results. On prolonging the dark interval sufficiently, the total O_2 -output within a given time becomes very small even under the condition of CO_2 -saturation, and it was practically impossible to follow the functional relationship between the maximum yield per flash and the concentration of CO_2 applied.

F. T. WALKER: The conditions of the culture solutions used, namely aeration and agitation, will alter the rate of CO_2 uptake. Were those factors taken into consideration in the experiments? We have found these factors materially affect normal and healthy growth and therefore photosynthesis of algae.

H. TAMIYA: All our experiments were carried out under the condition of CO_2 saturation, so that the velocity of CO_2 uptake could hardly have been rate-determining for the whole process. The algae used were all cultured under a certain specified condition, and no attempt was made to study the effect of different culture conditions.

E. C. WASSINK: I should like to remark that nowadays everyone is convinced of the fact that the "Blackman-reaction" is not one simple chemical process, so that the discovery of a new temperature sensitive reaction within this realm is not apt to discard every type of photosynthetic unit, *i.e.* cooperation and energy transfer between several chlorophyll molecules.

H. TAMIYA: We are wholly aware of the fact that the "Blackman-reaction" is not one simple process. What I concluded from our experiment is that there must occur, in certain stages of the photosynthetic process, a deactivation reaction of some photochemical intermediate, which we tentatively assumed to be the photoactivated form of chlorophyll. We do not deny the possibility of energy transfer between chlorophyll molecules. The essential point of the theory of "photosynthetic unit" may rather lie in its postulation that the energy transfer between a large number of chlorophyll molecules should occur "without any loss of energy." And this postulation, I think, may have lost its necessary ground in view of the fact established in our experiment.

L. R. BLINKS, FRANCIS HAXO
and C. YOCUM (Pacific Grove, Calif.)

Photosynthetic Action Spectra of Marine Algae

Relative photosynthetic rates of thin, flat marine algae were determined by a modification of the polarographic oxygen method, the thalli being in direct contact with a platinum cathode polarized at 0.5 volt. The increase of current in the light was taken as a measure of photosynthetic oxygen production. Absorption spectra of the same algae were taken in a modified Ulbricht sphere, monochromatic light for both absorption and action spectra being derived from a grating monochromator. About 35 points were plotted through the visible spectrum. Green algae (*Ulva*, *Monostroma*) showed close correspondence between action and absorption spectra, indicating a nearly equal effectiveness of all pigments. A

brown alga (*Coilodesme*) showed nearly as good correspondence, including the spectral region absorbed by the carotenoid, fucoxanthin.

A number of genera of red algae, however, displayed marked discrepancies between absorption and action spectra. The photosynthetic rates are high in the spectral regions absorbed by the "phycobilin" pigments (phycoerythrin and phycocyanin); in those algae containing largely the former (*Delesseria*, *Schizymenia*, *Porphyrella*), the maximum photosynthesis was in the green part of the spectrum, with peaks at 495, 540 and 565 m μ , corresponding to the absorption maxima of phycoerythrin. In the genus *Porphyra*, there is a series of three species with increasing phycocyanin and less phycoerythrin: the action spectra parallel this, with increasing photosynthesis in the orange-red region (600 to 640 m μ) corresponding to the broad absorption of phycocyanin. In all the red algae studied, photosynthesis was almost minimal at 435 m μ and 675 m μ , the chlorophyll absorption maxima. Although chlorophyll (and carotenoids) are present in red algae to about the same degree as in green and brown algae, the light absorbed by them is not efficiently used. Manometric determinations indicate that 10 to 12 quanta are required per oxygen molecule produced, throughout the spectrum in green and brown algae, and in the middle of the spectrum with red algae. But the efficiency falls greatly in the regions absorbed by chlorophyll and carotenoids, 30 to 40 quanta being required in blue or red light, by red algae.

Long sojourn (8 to 10 days), however, in either blue or red light, serves to activate the chlorophyll, and efficiency rises to almost normal values. A few hours exposure to green light then rapidly de-activates the chlorophyll. This effect is doubtless responsible for the behavior of naturally occurring red algae.

The paper was read by C. S. FRENCH.

Discussion

E. K. GABRIELSEN: In addition to this paper I should like to present some few data for

energy yields in green, brown, and red marine algae, and in green leaves (published in Nord. Förening f. Fysiol. Bot. medd. nr 2 1950). The table shows an extremely low value for energy yield in red light for the red alga (*Dilsea edulis*). The alga is only capable of transforming about 8% of the light energy to chemical energy, whereas the green leaves yield about 17%. Owing to the high chlorophyll concentration, in the alga as well as in the leaf, one should have expected nearly the same energy yield in both of these two photosynthesizing organs. So the data seem to verify Dr. BLINKS's findings that the chlorophyll in red algae does not work with the same efficiency as in other photosynthesizing organs.

E. C. WASSINK: I was struck by the fact that the figures for *Ulva* and *Sinapis* in the various spectral regions are strongly different. What may be the reason for this, since the pigment systems are fundamentally similar?

E. K. GABRIELSEN: The energy yields are computed on the basis of incident light and

the differences are due to the different light absorption (different thickness, different concentration of chlorophyll) in the two kinds of plants.

B. KOK: Do you know the method used by BLINKS and HAXO for the estimation of the absorption spectra presented in their paper?

C. S. FRENCH: A barrier layer cell covered by half of an integrating sphere was used with the alga on a glass slide on the face of the cell.

R. EMERSON: The application of a photonic cell to the technique of integrating scattered light does not appear to be entirely satisfactory, since the response of the barrier layer type of cell may vary considerably with the distribution of the energy over the sensitive surface.

C. S. FRENCH: I should think that such errors were probably avoided in this work by control experiments with transparent, and with translucent, but non-absorbing materials put in place of the algae to estimate the possible magnitude of such errors.

SESSION 3

July 14th, 2—4 p. m.

Chairman: H. TAMIYA

SUBJECT:

Photosynthesis

E. C. WASSINK (Wageningen)

On Phosphate Exchanges Accompanying Photosynthesis

In a study on phosphate exchanges in connection with conditions for photosynthesis, reported on previously (WASSINK, TJIA, WINTERMANS: Proc. Kon. Akad. Amsterdam 52, 412-422, 1949), purple sulphur bacteria had been used as object mainly for the following reasons: 1) Their relationship to *Thiobacillus*, the organism at which VOGLER, c.s. demonstrated the rôle of phosphate exchange in the connection between energy producing and energy consuming processes. 2) They allowed

a separate study of the influence of CO_2 and the reductant (H_2) in light and darkness. 3) The effect of these agents on photosynthesis had been extensively studied before. The chief results were that absence of CO_2 in light was rather neutral as to phosphate exchange whereas, in dark, phosphate was always liberated. These results could be interpreted along the lines pointed out by VOGLER, c.s. The measurements were made in borate buffer, pH 8.0. Some preliminary experiments were made in which uptake of gas and phosphate exchange were followed simultaneously under different conditions.

Similar experiments have now been made

with *Chlorella* by the same investigators. The charm of this organism was that it was known to stand well dilute solutions so that, probably, no buffers had to be added. In preliminary experiments in tap water with small amounts of phosphate, results indicating strong phosphate uptakes were obtained if the suspension was ventilated in the light with air not containing any CO_2 . It soon turned out, however, that the "uptakes" surpassed reasonable limits, and it was made probable that they were partly simulated by disappearance of phosphate from the suspension medium by inorganic precipitation, owing to increase in pH of the medium by the metabolic activity of the cells under the conditions chosen.

Advance was made by securing cells containing little phosphate and working at slightly buffered, low pH ($\text{K}_2\text{SO}_4 + \text{H}_2\text{SO}_4$). Borate buffers were not stood very well. In addition, phosphate determinations were made in T.C.A.-treated samples of suspension. The procedure had to be rigorously standardized.

In darkness, *Chlorella* shows slight conversion of phosphate from T.C.A.-labile into T.C.A.-stable form. In light, this conversion is increased. This increase is small in the presence of 5% CO_2 (in air), much greater in the absence of CO_2 . Thus, apart from minor deviations, the situation is analogous to the one found in *Chromatium*. Light, and absence of CO_2 , causes the largest conversion of inorganic phosphate into—as is now shown—T.C.A.-stable form. One may speculate that the compounds formed have something to do with the generation of "reducing power" by light, as pointed out by WASSINK *et al.* (1938-39), and CALVIN, *c.s.* (1948).

The methodical difficulties mentioned above seem to be related to those encountered by GEST and KAMEN (*J. Biol. Chem.* 176 [1948]).

Our measurements were made with a colorimetric method. It should be pointed out that application of tracer-P, which is planned for a further phase of this study, would not have offered a guarantee against the pitfalls encountered.

Finally, one should observe that, if the above studies had been undertaken from the viewpoint of permeability or ion uptake, one would have concluded that CO_2 influences the permeability for phosphate in the light only. It would seem that a much better understanding is obtained if the involvement of the permeated ions in metabolic processes is considered as a major factor in the uptake process.

M. CALVIN (Berkeley, Calif.)

The Path of Carbon in Photosynthesis

The intermediates involved in the incorporation of carbon dioxide by photosynthesizing green plants have been investigated by the aid of radioactive carbon dioxide. The design of the experiment was straightforward. A variety of plants were fed the labelled carbon dioxide for varying periods of time (all less than five minutes) under a diversity of conditions. The plants were then killed and the distribution of radioactivity among the plant constituents was determined. The methods used in this determination ranged from macroscopic isolation procedures involving extraction and crystallization through ion exchange separations to paper chromatography. The last mentioned method has so far proved to be the most expedient and useful.

In addition to determining which compounds had become radioactive, a number of them were degraded in such a manner as to allow the determination of the distribution of radioactivity amongst the carbon atoms of any given compound. This information has permitted the proposal of a four carbon cycle including two carboxylation reactions which provide the structural raw materials for the synthesis of the three major constituents of plants—fats, carbohydrates and proteins. It is interesting to note that radioactivity appears in all three of these groups in as short a time as 120 seconds of photosynthesis.

The essentials of the cycle are the carboxylation of a two carbon compound to form a

three carbon compound followed by the carboxylation of a three carbon compound to form a four carbon compound and the splitting of the four carbon compound to regenerate ultimately two of the original two carbon carbon dioxide acceptors. Each of these three classes of compounds, namely, the two, three, and four carbon compounds, undergo a number of transformations and rearrangements within themselves to prepare them for their transition to the next class.

Of the three major plant constituents only some members of the carbohydrate class have been investigated sufficiently completely to allow the detailed specification of their synthesis. This has been carried out particularly with sucrose and some dextrans.

CONSTANCE E. HARTT and G. O. BURR
(Honolulu)

Photosynthesis by Sugar Cane Fed Radioactive Carbon Dioxide

Radioactive carbon dioxide prepared from radioactive barium carbonate obtained from the U. S. Atomic Energy Commission at Oak Ridge, Tennessee, has been fed to leaves of the sugar cane plant in natural and artificial light, for the purpose of studying the formation of sugars and other products. Matched portions of blades were fed for 10 minutes in total darkness, followed by periods in the light ranging from five seconds to five minutes. The major fractions extracted and counted with Geiger counters were: 95 per cent alcohol extract, ammonium oxalate extract, water extract, acid hydrolysate, cellulose, lignin and ash. Fractions of the 95 per cent alcohol extract included: petrol ether extract, water-insoluble constituents, ether extract, substances insoluble in cold 95 per cent alcohol, the barium-zinc precipitate, glucose, fructose and sucrose. After treatment with cation and anion resins and such as the reducing sugars were separated from sucrose chromatographically. Total and reducing sugars were analysed quantitatively by the micro-ferricyanide meth-

od, and fructose by the Seliwanof method. Glucose, fructose and sucrose were crystallized after the addition of carrier sugars and were converted to osazones which were recrystallized to constant radioactivity.

The chief product of dark fixation of carbon dioxide by the sugar cane plant is the ammonium oxalate extract, which is chiefly pectic substances. Other fractions radioactive in the dark are the alcohol extract (particularly the cold 95 per cent alcohol-insoluble, the water-insoluble, and the ether extract), also the water extract and lignin. All these fractions increase in radioactivity when the leaves are exposed to light, but the greatest gain is made by the alcohol extract. The acid hydrolysate becomes radioactive after five seconds and cellulose after 15 seconds. Glucose had the highest specific activity of the three sugars and gained in radioactivity (both specific activity and total counts) before any gain in sucrose, for which reason the conclusion is drawn that glucose is the first free sugar formed in photosynthesis by the sugar cane plant, followed by fructose, then sucrose. At 10 seconds, 100 per cent of the gain in sugars was due to glucose plus fructose; while at five minutes, 80 per cent of the gain in sugars was due to sucrose. Sucrose is therefore a storage product, its formation starting at about the same time as the formation of the acid-hydrolyzable pentosans and cellulose.

The paper was read by Dr. HARTT.

CONSTANCE E. HARTT and G. O. BURR
(Honolulu)

Translocation by Sugar Cane Fed Radioactive Carbon Dioxide

Radioactive carbon dioxide obtained from the U. S. Atomic Energy Commission at Oak Ridge, Tennessee, has been used at the Experiment Station of the Hawaiian Sugar Planters' Association since March 1947, to find out where the material synthesized in a particular leaf is stored and used and to study

the rate of translocation. Geiger counts made on the alcohol extracts and residues of blades, sheaths, stems and roots prove the universal distribution of the products of photosynthesis from a single blade throughout the entire plant. In 20 hours, material manufactured by a blade of one stalk had reached the blades of sister stalks of the same plant. In 44 hours, 94 per cent of the photosynthate had been translocated out of the fed blade, and in eight days, 97 per cent had been translocated out of the fed blade. The part of the plant which received the greatest amount of photosynthate was the stalk immediately below the joint to which the fed blade was attached. Even the old joints were radioactive, which disproves the theory that active storage takes place only in the joints to which leaves are attached. Sister stalks varied considerably in total counts received by translocation, and this variation had no apparent connection with size of stalk, which indicates that there are internal anatomical or physiological factors, not seen by casual inspection, which result in unequal distribution of the photosynthate. This indicates a keen competition among the stalks of a stool. Photosynthate made by the upper half of a single blade fed radioactive carbon dioxide was respired by the roots six hours later. Total distance from place of feeding to place of respiration was 258 cm. Since the six hour time interval included the time required for photosynthesis in the leaf and for respiration in the root the minimum estimate for rate of translocation is 43 cm per hour or 0.7 cm per minute.

The paper was read by Dr. HARTT.

D. I. ARNON (Berkeley, Calif.)

Extracellular Reactions of Chloroplasts

I. Oxygen Evolution in the Light.

II. Oxygen Uptake and Carbon Dioxide Evolution in the Dark

As part of a general investigation of the function of micronutrients in plant nutrition

we undertook to explore certain phases of photosynthesis. Our attention was centered on the reactions and properties of chloroplasts and chloroplast fragments since these are the only subcellular bodies known today to be capable of carrying out *in vitro* the reaction characteristic of photosynthesis in green plants: the photolysis of water with a resultant evolution of oxygen.

Our experimental approach has been to study the enzymatic reactions of chloroplast fragments of *Beta vulgaris* both in the light and in the dark. It was found that in the leaves of that species, the copper enzyme, polyphenoloxidase was concentrated in the chloroplasts rather than in the cytoplasm. In the dark, the chloroplast fragments exhibited an *endogenous* respiration-like activity: a marked oxygen uptake and a slight carbon dioxide evolution. This respiratory gas exchange of the chloroplasts was sharply increased by the addition of a boiled extract of the cytoplasmic fraction. The effect was particularly great in enhancing the carbon dioxide evolution. The respiratory activity of the chloroplast fragments was completely stopped by boiling and was inhibited by iodoacetamide, azide, fluoride, diethyldithiocarbamate and dinitrophenol. The optimum pH for both oxygen uptake and carbon dioxide evolution was around pH 5.

In the light, the same chloroplast preparation evolved oxygen and gave stoichiometric yields with three oxidants, o-quinone, ferricyanide and phenol indophenol thus confirming results obtained by other workers. Support for the identity of the oxygen-liberating mechanism in isolated chloroplast fragments with that in the intact green cells was found in the inhibitory effects of hydroxylamine and phenylurethane. Chloride was found to be an essential component of the *in vitro* system but the evidence obtained suggests that this ion is not involved in photosynthesis *in vivo*. The photolytic reaction was inhibited by o-phenanthroline and potassium ethyl xanthate but the inhibition was reversible either

by dialysis or by the addition of metals. These results are interpreted as consistent with a theory that the light reaction in photosynthesis involves a metal catalysis through a metalloprotein enzyme and that the metal concerned is one which like iron or copper is capable of undergoing oxidation-reduction. A fuller account of this work will be found in the following references.

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Discussion

J. B. THOMAS: Did you study whether the chloride and the metals you mentioned increase the heat stability of the system?

D. I. ARNON: The destruction of the system at the higher temperatures appears to be irreversible, and I doubt whether chloride or metals can reactivate it, although no systematic study of this was made.

C. S. FRENCH: Does the reversal of inhibition by the addition of a metal indicate that this metal has a definite function in the reac-

tion or does it merely act as a means for removing the poison?

D. I. ARNON: In our experiments the evidence suggests that the addition of the metal served as a means for removing the poison. We hope, however, to obtain some indication of the metal involved in the photolytic reaction of chloroplasts by using different metal poisons of varying specificity toward different metals. Thus, xanthate is regarded as being especially effective in combining with copper.

G. LATTES: Was the intermediation of a metal protein in the photolysis of water considered to occur in higher plant photosynthesis, in the Hill reaction, or in both?

D. I. ARNON: It is considered that the Hill reaction corresponds to the reactions associated with the photolysis of water in higher plant photosynthesis. Hence a metal protein essential for the Hill reaction would also be essential for photosynthesis in intact plants. It must be stressed, however, that at this time the status of the postulated metal protein is a mere working hypothesis.

H. BURSTRÖM: Do your results suggest that a major part of the normal respiration in the leaf is confined to the chloroplasts?

D. I. ARNON: Our results suggest that the chloroplasts contain enzymes capable of oxygen uptake and CO_2 evolution in magnitudes, sufficiently large, when expressed on a unit chlorophyll basis, to be comparable with the endogenous respiration of leaf discs. Whether the respiration-like activity of isolated chloroplasts is in fact identical with that of intact leaves, remains to be established by future experiments.

SESSION 4

July 17th, 9—11 a. m.

Chairman: F. G. GREGORY

SUBJECT:

Photosynthesis, Carbohydrate Metabolism

E. K. GABRIELSEN (Köbenhavn)
On the CO₂-Threshold in Photosynthesis of Leaves

Fifteen years ago MILLER and BURR showed that potted plants could not reduce the carbon dioxide concentration to lower values than 0.010 vol.-percent when illuminated at high light intensity in a closed system. Their experimental material included 10 species of widely different types of leafy plants.

MILLER and BURR assumed that their results were valid only for whole potted plants, i.e., that the observed limit was an expression for a balance between photosynthesis and CO₂ production from respiration in stems and roots, shaded leaves, and microorganisms in the soil. However, in 1947 I have found that the same limitation for CO₂ uptake exists when a single, excised green leaf is used for the experiment. Also, I have been able to demonstrate an accumulation of respiratory carbon dioxide when the same kind of leaves are exposed to light in CO₂-free air; the accumulation continued until a level about 0.010 vol.-percent CO₂ was reached.

In order to explain the limitation of the CO₂ uptake two hypotheses have been proposed: 1) The compensation point hypothesis explains the limit value as caused by an equilibrium between the rates of photosynthesis and respiration. 2) The threshold value hypothesis postulates that no photosynthesis takes place before a certain concentration of carbon dioxide (equal to the observed limit for CO₂ uptake) is obtained in the green cells.

The second hypothesis is supported by the following facts: 1) MILLER and BURR found

the same limit value for CO₂ uptake when using different types of plants. It must be assumed that the rate of respiration and also that of photosynthesis has varied from plant to plant, and it seems impossible that these different rates could result in exactly the same equilibrium value. 2) Furthermore, MILLER and BURR showed that the CO₂ balance was not altered by considerable changes in temperature. It is well known that the respiration rate is more affected by temperature changes than the photosynthesis rate. Therefore, a change of temperature should result in an increased equilibrium value if the compensation point hypothesis were valid. 3) It has been demonstrated (GABRIELSEN 1949) that photosynthesis in a current of CO₂-free air depends upon the rate at which carbon dioxide is produced in the leaf and upon the rate at which this gas is transported from the leaf to its surroundings. If the respiration rate is low, and/or the possibilities for carbon dioxide to escape are great, no photosynthesis takes place. This strongly supports the second hypothesis.

Discussion

E. C. WASSINK: I should like to ask Dr. GABRIELSEN whether his first possibility is still conflicting with Prof. CALVIN's results if "the rate of respiration" is substituted by the "rate of coming-out or diffusion" of CO₂.

E. K. GABRIELSEN: In so far as I understand the question, I think there will be no difference.

O. V. S. HEATH: I have obtained, by a completely different method, an almost exactly similar value of 0.01 per cent for the minimum CO₂ concentration in the intercellular

spaces of leaves during photosynthesis. Since the same value was obtained for such very different species as *Begonia* and *Pelargonium*, a simple equilibrium between respiration and assimilation seemed to me, as to Prof. GABRIELSEN, unlikely to be the cause. I have therefore suggested a third hypothesis, viz. that there is at the mesophyll cell surface a "buffered" tension of CO_2 maintained at a value in equilibrium with 0.01 % in the air. If, in moving CO_2 -free air experiments, the CO_2 output in light equalled but never exceeded that in the dark, no matter how much the flow was increased, this would be consistent with the threshold value hypothesis. If, however, a sufficiently high flow rate gave more CO_2 in light than in darkness, an effect of light in increasing respiration would be shown, with the implication that in Prof. GABRIELSEN's closed system experiments, where CO_2 output was found to be the same in light and darkness, some reassimilation was occurring. This would be opposed to the threshold value hypothesis.

E. K. GABRIELSEN: I am very glad to hear that Dr. HEATH in his interesting experiments has found results which are in agreement with those I have obtained. Dr. HEATH's suggestion about the "buffer" needs further consideration, and I will bear it in mind for coming experimental work.

J. H. C. SMITH (Stanford, Calif.)

Chlorophyll Formation and its Correlation with the Development of Photosynthetic Activity

Because the ability of etiolated plants to photosynthesize is developed concurrently with the accumulation of chlorophyll, it seemed probable that an analysis of chlorophyll formation and its correlation with the development of photosynthetic activity would yield a better understanding of the pigment's participation in photosynthesis.

For this reason, some of the steps leading

to chlorophyll formation and accumulation in etiolated seedlings have been examined and correlated with the genesis of their oxygen-liberating capacity.

Etiolated seedlings contain protochlorophyll. By illuminating the seedlings, this pigment is converted by photochemical action to chlorophyll *a*. This has been shown (a) by demonstrating the quantitative relationship existing between the disappearance of protochlorophyll and the appearance of chlorophyll *a* during the conversion, and (b) by the similarity of the action spectrum for the transformation to the absorption spectrum of protochlorophyll.

In the beginning of greening, only chlorophyll *a* is formed. When a certain quantity of chlorophyll *a* has been produced, then chlorophyll *b* appears. Thereafter, chlorophyll *b* and chlorophyll *a* are formed in constant proportion to each other. These results are little affected by change of temperature or by illumination with intermittent light.

The development of oxygen-liberating capacity in etiolated leaves has been examined at each of these stages in the development of chlorophyll. It has been found that no oxygen is liberated from leaves during the photochemical conversion of protochlorophyll to chlorophyll *a*. Even when leaves contain appreciable quantities of chlorophyll *a*, derived from the conversion of the protochlorophyll initially present, they fail to liberate oxygen on being illuminated. A sojourn in the dark produces this capacity even though the chlorophyll content is not increased. A short period of illumination subsequent to the sojourn in the dark augments greatly the oxygen-liberating capacity of the leaves. The ability to liberate oxygen is not dependent on the presence of chlorophyll *b*.

When leaves are greened in continuous light, their capacity to evolve oxygen is increased in direct proportion to the chlorophyll content of the leaves exclusive of the chlorophyll formed from the conversion of the initial protochlorophyll. When leaves are greened with

equal periods of illumination separated by dark periods of various lengths, the oxygen-evolving capacity is increased also in proportion to the total chlorophyll formed subsequent to that formed by the conversion of the initial protochlorophyll.

These facts demonstrate that following a short irradiation it is necessary for dark-grown leaves to form substances other than chlorophyll or to organize the material they contain in order to acquire the capacity to liberate oxygen. These changes can take place at least partially in the dark.

Whether certain other processes known to occur during greening are involved in the development of oxygen-liberating capacity is yet to be determined.

Discussion

M. CALVIN: Did you follow the carotenoid content with O_2 evolving capacity?

J. H. C. SMITH: We have no experiments correlating carotenoid formation and photosynthetic activity. It is difficult to obtain such data, because the increase in carotenoids is small, at most under conditions used by us, and probably falls within experimental error of determinations made.

J. B. THOMAS: Perhaps it may interest you that the assimilatory quotient is shifting during the beginning of the process of chlorophyll formation.

J. H. C. SMITH: It is not surprising that the photosynthetic quotient varies in the beginnings of photosynthesis by illuminated, etiolated leaves. The amounts of oxygen evolved are very small and undoubtedly the respiration continues so that abnormal relationships exist.

R. EMERSON: Would it be correct to say that the beginning of the capacity for photosynthesis coincides with the beginning of formation of chlorophyll *b*?

J. H. C. SMITH: It appears that oxygen evolution begins before significant quantities of chlorophyll *b* are found. Certainly it begins before the amounts detected in our experiments made their appearance.

J. S. LOWE (Nottingham)

The Enzymic Absorption of Sugars by Excised Roots

Excised roots of *Lycopersicum esculentum*, *Helianthus annuus*, *Medicago sativa* and *Raphanus sativus* were grown in WHITE's culture medium in order to investigate the absorption of carbohydrates by parenchymatous root cells. There was a marked similarity in response to experimental treatment in all four species.

Sucrose was the only sugar capable of maintaining healthy growth over several passages. Glucose inhibited the growth of *Lycopersicum* and *Medicago* even in the presence of sucrose.

The growth response to variations in pH of the medium gave results which resembled the typical pH/enzyme activity relationship. There was a marked optimum at pH 4.7-4.9.

Phloridzin inhibited the growth of all excised roots. The inhibition was

a) proportional to the concentration of phloridzin,

b) affected by the ratio of sucrose to phloridzin present in the medium,

c) completely reversible.

Phloridzin was found not to penetrate into the root cells and therefore must be considered to act at the cell surface.

Sucrose utilization as measured by O_2 uptake was found to occur only in the presence of inorganic phosphate.

These four lines of evidence support the hypothesis that an enzyme sucrose phosphorylase exists at the surface of root cells of these dicotyledonous species.

Excised roots of *Secale cereale* were grown in BURSTRÖM's culture medium. Glucose, fructose, sucrose and raffinose supported satisfactory growth.

The growth in the glucose medium was not affected by pH within the limits pH 4.2-6.2; but in the sucrose medium there was a marked pH optimum at about pH 4.8.

Phloridzin inhibited growth in proportion to its concentration; the concentration of glu-

cose present did not affect the degree of inhibition.

To account for these results, the enzymes invertase and hexokinase are postulated as occurring at the surface of *Secale* root cells.

It is concluded therefore that surface active enzymes are primarily responsible for the entry of sugars into the cells of roots.

H. SAID (Cairo)

Sucrose Inversion and Absorption by Plant Tissues

I have repeatedly established that when discs from storage organs or cut ends of plant leaves were dipped in aqueous sucrose solution, the latter was always inverted in the medium before its absorption by plant tissue cells. The rate of inversion was always faster than the rate of absorption, hence the accumulation of reducing sugars in the culture medium. I have also shown that a fructofuranosidase enzyme was responsible for the sucrose inversion at the outer cytoplasmic surfaces of the cells which were in contact with the sucrose solution in the medium.

On the other hand, DORMER and STREET (1949) postulated the existence of another mechanism (*i.e.* phosphorylysis) involving the breakdown of sucrose into its hexose units in the culture solution of excised tomato roots.

I have results of a number of experiments which seem to oppose the conclusions of DORMER and STREET.

The first point to be considered is that the suggested sucrose phosphorylase is strictly specific to sucrose alone. If, therefore, a mechanism as suggested by DORMER and STREET is operative at the cell surfaces, we should expect that aqueous solution of another fructoside like raffinose would not be broken down when coming in contact with the cytoplasmic surfaces of discs from carrot or radish roots. I tried this and found that raffinose started with no direct copper reducing value, but after being in contact with carrot discs, there was rapid hydrolysis of raffinose and accumu-

lation of reducing sugars (presumably fructose and melibiose) in the external medium. This indicated definitely that hydrolysis of sucrose and raffinose was by fructofuranosidase enzyme and not by phosphorylase enzyme.

DORMER and STREET claimed to have found evidence against an extracellular inversion of sucrose independent of hexose absorption, and suggested that the breakdown of sucrose was linked with sugar absorption. That sucrose inversion may proceed at the cytoplasmic surfaces independent of sugar absorption is established from experiments in which I floated samples of carrot discs on sucrose solutions, some being aerated with air or oxygen while others being deprived of oxygen by bubbling pure nitrogen gas through the culture solutions. There was no sugar uptake under anaerobic conditions, and yet sucrose inversion went on to completion, though at a slightly lower rate than in air or oxygen atmospheres; the products of inversion were left entirely in the external medium.

I have also made experiments in which the rates of sucrose inversion and sugar absorption by carrot discs were tested in the presence of potassium and calcium salts. In all cases calcium salts seemed to depress both the rates of sucrose inversion and sugar absorption, but the depression of inversion was much greater than the depression of sugar uptake. Potassium salts, on the other hand, favoured slightly the sugar uptake but the rate of sucrose inversion was almost the same as that obtained by carrot discs floated on sucrose alone.

Discussion

During the joint discussion of J. S. LOWE's and H. SAID's papers LOWE remarked: The fact that Dr. SAID's material could utilize several sugars shows that we have discussed different processes. My material would not use glucose for healthy growth, nor could any of the other sugars, except sucrose, be utilized.

H. SAID asked if J. S. LOWE had tried to feed his excised roots on raffinose and then tested whether or not raffinose has been

hydrolysed at the surface of the plant cells. If such hydrolysis takes place, then this would indicate the occurrence of fructosidase enzyme, not phosphorylase.

A. ALMESTRAND then put the following question to J. S. LOWE: Have the roots of rye in glucose, sucrose, and fructose been investigated histologically? I have found that excised roots of barley and oats cannot grow for more than 10–15 days. There is cell elongation, but no cell divisions in the meristem. I have found a pH optimum of 5.0 for oat roots.

J. S. LOWE: I do not profess to be a histologist, but as far as I could detect, the roots of rye grown in glucose or sucrose media remained perfectly healthy. There was no inhibition of the meristematic activity nor a decrease in size of the meristem. I have not studied barley and oats, but the story for maize appears to be similar to that for rye. Wheat roots have a somewhat different story.

H. BURSTRÖM: The story of wheat is rather important, in so far as wheat roots utilize glucose but are even inhibited by sucrose. Nevertheless, sucrose is hydrolysed ten times more rapidly by wheat than by rye roots. If absorption, as probable, means utilization, this indicates that inversion is separated from absorption also in roots in this instance. — The salt action was observed by me long ago, and explained by changes in the surface charge of the cytoplasm by exchange of cations for H-ions on the cytoplasmic surface according to LUNDEGÅRDH, the surface pH regulating the enzyme activity.

S. TONZIG (Milano)

The Significance of Ascorbic Acid in Plants

The elongation of the cell under natural conditions should be regarded as regulated not solely by growth substances, but also by the contemporary presence of two contrasting, mutually-controlling classes of substances. A widespread component belonging to the class of anti-auxinic substances seems to be the ascorbic acid (AA). It is an established fact

that the most remarkable action exerted by growth substances on the plasma is expressed through a structural modification of the latter. This manifests itself as a viscosity alteration and as an increase in the dispersion and water absorption grades of the plasma colloids. Viscosity, water-absorption and dispersion grades are altered in the opposite direction by AA, which furthermore impairs or even eliminates the auxinic effects on growth. The cell's sensitiveness to other stimuli is simultaneously reduced. In plants the AA follows a given topographical distribution, and it has been found that the higher the AA content, the lower the plasma's viscosity and water-absorption grades, as well as the sensitiveness of the organ. The natural site where AA is formed is the leaf exposed to light, whence it migrates into the stem. In the latter, however, the AA motion is mainly acropetal, being considerably slow when going downward, so that almost no AA can be found in roots. In fact, plasmatic viscosity and water-absorption grades are much higher in roots, which are also far more sensitive than the stems to growth substances as well as to other stimuli, such as colchicin, etc. Plants growing in the dark have little or no AA even in their aerial parts (this being a typical condition in etiolated plants); at the same time plasmatic viscosity increases and stem sensitiveness to natural stimuli (abnormal elongation of internodes) is enhanced. The same is true for experimental treatments such as geotropical and phototropical stimuli, treatments with growth substances, colchicin, etc. If, on the contrary, the AA content in the stem is experimentally increased, then the plasmatic viscosity is lowered, stem elongation is stopped and sensitivity to both natural and experimental stimuli is markedly reduced. Even plants grown in the dark and experimentally enriched in AA content show normal internodal length. Increase of AA content in roots produces a lower plasmatic viscosity and such a severe reduction of sensitivity that geotropical reaction is nil and in some cases

even negative. Their elongation however is greater than in the control. A striking evidence for the sensitivity-reducing action exerted by AA on roots is given from the inhibition of formation of *Rhizobium* nodules in leguminous plant roots. On the other hand, in etiolated leguminous plant stems a cellular proliferation after a *Rhizobium* inoculation is noted. In pendulous-branch forms of plants normally having erect branches (*Sophora*, *Morus*), the pendulous branches have a more viscous plasma and a lower content than normal, erect branches even in the same individual when the pendulous form is grafted on an erect-branch stock. The AA treatment of terminal buds (*Capsicum*) causes the development of lateral buds below, which would be otherwise inhibited. AA and growth substances exert an opposite action on water-absorption as well as on plasmatic permeability. Actually organs enriched with AA or IAA (segments of *Lupinus* hypocotyl, oats coleoptile) dehydrate by drying at a rate respectively faster and lower than controls. On the other hand, an IAA treatment will stimulate guttation (intact oats coleoptiles) and bleeding (excised *Ricinus* hypocotyls) phenomena; both are, on the contrary, inhibited by AA treatment. The mechanism of AA action is still in work; the only established fact is that the growth substances are not destroyed by it. A far larger amount of auxin than from controls is obtained, even by means of simple

diffusion on agar, from organs (oats coleoptiles) treated with AA. This experiment seems to indicate the AA's tendency to detach the auxin from the active auxin-protein complexes, thus inactivating them. The reduced permeability, moreover, makes slower the transport of growth substances. Another effect exerted by AA, this one affecting photosynthesis, is represented by the larger amount of total chlorophyll in AA-enriched plants, and by the increased chlorophyll *a*/chlorophyll *b* and carotene/xanthophyll ratios. An increase in the AA contents is noted during the spring-summer period in ligneous plant leaves, while the leaf pigments vary as described above and branch lengthening slows down until it finally stops.

Discussion

CORNELIA A. REINDERS-GOUWENTAK: Dans les tubercules de *Solanum tuberosum* on trouve des substances de croissance ainsi que des substances inhibitrices et l'acide ascorbique. Laquelle est la relation entre ces trois espèces de substance au point de vue de votre contribution d'aujourd'hui?

S. TONZIG: L'acide ascorbique est seulement un représentant de la catégorie des substances inhibitrices, mais je crois même qu'il y a plusieurs types de substances inhibitrices. Nous savons en effet qu'il y a plusieurs blastocolines, mais spécifiques pour les diverses plantes. L'acide ascorbique est au contraire très répandu presque dans tous les plantes vertes.

SESSION 5

July 17th, 1—4 p. m.

Chairman: K. V. THIMANN

SUBJECT:

Stomata, Respiration, etc.

O. V. S. HEATH (London)

Control of Stomatal Movement by Carbon Dioxide and Other Factors

Recent work (1) with *Pelargonium* and wheat leaves has shown that the stomata are very sensitive to reduction of the external CO₂ con-

centration below the normal 0.03 %, opening widely under such conditions. The CO₂ concentration is operative in the substomatal cavities, for if *Pelargonium* stomata are completely closed, in darkness, external CO₂ concentration is without effect.

In experiments with wheat leaves (2) the

interrelations of CO_2 concentration, rate of air flow and light intensity were investigated. Marked stomatal opening occurred with reduction of CO_2 content to 0.01 %, but below this concentration no further opening was found. This maximal opening at 0.01 % CO_2 is of interest in view of the finding by GABRIELSEN (3, 4) and by the author (5, 6) that photosynthesis can reduce the CO_2 in the intercellular spaces to 0.01 % but no further. Light intensity showed virtually no interaction with CO_2 , the light effect being as large at 0.01 % CO_2 as at any other concentration. This suggests a direct effect of light on the stomata, independent of that acting through photosynthesis by the mesophyll and the CO_2 concentration in the substomatal cavities. The theory that stomatal control is entirely due to the latter thus appears inadequate. In these experiments with wheat, increased rate of air flow caused partial stomatal closure, even with 0.01 % or zero CO_2 , and further experiments with moist and dry CO_2 -free air showed that this was due to drying.

In *Pelargonium* (1) this closing effect of dry air is not found, but there is a remarkable effect of humidity on rate of response to all the other stimuli investigated, both opening and closing being more rapid in dry than in moist air.

Experiments with onion leaves showed: a) that onion stomata respond to light, although devoid of both chloroplasts and starch so that a starch-sugar mechanism cannot be concerned; b) that raising the temperature above about 25° C causes marked stomatal closure. This temperature effect may perhaps be attributed to the CO_2 of respiration of the guard cells, re-inforced by that of the bulky non-chlorophyllous tissue in the leaf. Accumulation of CO_2 in the hollow leaf may also account for the great delay observed in opening on illumination as compared with *Pelargonium*.

Most of the effects described appear to have the biological advantage of causing stomatal closure under conditions conducive to rapid water loss.

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Discussion

M. G. STÅLFELT: May I ask if you know anything about the water deficit of your objects? I have found that stomata closure sets in when water deficit increases above the level of a few per cent of the water capacity of the leaf, that this water-induced reaction is governing the stomata movements and that it is more effective than the other reactions of the opening-closing system. Now the water deficit is a function of other factors, also the evaporation, but the evaporation is the result of temperature, humidity and the flow of the air, i.e. the factors investigated by Dr. HEATH.

O. V. S. HEATH: The water deficits of the leaves were not determined in the experiments now under discussion. Attached leaves on well-watered, potted plants were used. It does not appear that water deficit could have been concerned in the responses to CO_2 or to light (except perhaps in the rate of response) for similar effects were found in moist and in dry air. I showed experimentally that the closing effect on wheat stomata of increased rate of flow of dry air was due to desiccation rather than to CO_2 , and I suggested that the high temperature effect on onion stomata might also be a desiccation effect though I preferred to interpret it in terms of CO_2 of respiration. The desiccation effects on the stomata depend, however, on the water relations of the epidermis rather than of the leaf as a whole (cf. WILLIAMS, J. Exp. Bot. 1950) and with rapidly changed conditions it may be doubted if determinations of water deficits would do much to elucidate the problem.

L. BRAUNER: Would you consider the possibility of changes of the water permeability as a contributory factor in the stomatal mechanism?

O. V. S. HEATH: Although I think we have evidence of a direct effect of light on the stomata, I have no evidence as to its mechanism. I have suggested that photosynthesis by the chloroplasts in the guard cells might be concerned. I do not see how a change in water permeability could do more than change the rate of movement, but a change in permeability to solutes could, of course, cause a change in direction and magnitude of movement. Here, however, two difficulties seem to arise:—if solutes are lost from the guard cells during closure owing to increased permeability, where do they go to, and how are they regained for opening to occur once more?

K. V. THIMANN: Do you think that your findings bear on those of MASKELL, who showed a "daily march" of photosynthesis in leaves corresponding to movement of stomata? His measurements were made under an enlarged porometer cup. Or do you consider his plant (*Prunus laurocerasus*) may have behaved differently from wheat?

O. V. S. HEATH: MASKELL left his porometer cup in position on the leaf throughout an experiment and it seems most probable that the stomata within the cup area behaved differently from those outside, though it is possible that cherry laurel stomata are insensitive to CO_2 . His very consistent results suggest, however, that the stomata both inside and outside the cup followed a diurnal rhythm similar in phase, though the magnitudes of the apertures may well have differed.

B. HUBER: Would you be able to give some advice for practice of porometer measurements? It would be terrible for ecologists if we could hope no longer to measure the natural width of stomata with a porometer. Is it possible to prevent the CO_2 -deficit inside the porometer-cup?

O. V. S. HEATH: The CO_2 -deficit inside the cup can be prevented in either of two ways:

a) by sweeping out the cup between porometer readings with a stream of ordinary air such as surrounds the rest of the leaf. The rate of sweeping does not appear to be very critical, but it is possible to cause differential changes if it is very slow or perhaps if it is very fast, and it is therefore better to use a detachable cup such as that devised by professor GREGORY (GREGORY *et al.*, J. Exp. Bot. 1950). Here a gelatine washer remains in contact with the leaf throughout, but the lower part of the cup can be removed between readings, thus exposing the portion of leaf within the washer to the external air.

H. ULLRICH: Wie gross waren die Durchmesser während der Versuche, absolut gesehen?

O. V. S. HEATH: We have not yet calibrated the porometer in terms of actual stomatal aperture, nor is the much more important calibration in terms of stomatal diffusive conductance yet completed. Extensive data collected for the former calibration in terms of aperture as obtained by HOYD's method have proved worthless, for I have since found that in *Pelargonium* apertures given by HOYD's method are much wider than those on the living leaf. I have therefore no data for the actual stomatal dimensions in these experiments.

T. H. VAN DEN HONERT (Leiden)

Quantitative Considerations in Stomatal Transpiration

The thickness of an adhering air layer over an evaporating water surface in still air may be approximated by means of the diffusion constant of water vapour in air. It is of the order of several millimetres to 1 cm.

As RENNER (1910) clearly pointed out, such a still air layer ("Dampfkuppe") must also constitute a diffusion resistance over a transpiring leaf, a fact overlooked by BROWN and ESCOMBE (1900) and since by many others.

The following is a report on experiments mainly made by G. G. J. BANGE, Leiden, who investigated, with the above idea in mind, the

question whether stomatal transpiration could be quantitatively explained as a diffusion of water vapour in air.

Stomatal transpiration rates from leaf discs (surface 5 cm^2) of *Zebrina pendula* were determined by weighing. Evaporation from the cut edge was duly prevented. Very short transpiration times were taken to minimize the temperature decrease. One series of determinations was made in still air, another in wind. The water loss was expressed in terms of $\text{g } 10^{-6}$ per second per cm^2 per per cent rel. humidity deficit. Apertures of 25 stomata were measured microscopically and the number of stomata per cm^2 determined in the same leaf sample.

Besides, size and shape of transverse sections of the stomatal pores and the substomatal air spaces were measured and simplified into geometrical figures.

As Ohm's law for the electric current and Fick's law for diffusion are essentially similar, an analogon of Ohm's law may be applied here. So in a series of 4 consecutive resistances, viz. 1) substomatal air spaces, 2) stomatal pores, 3) individual vapour cups over stomata and 4) adhering air layer, respectively, the total diffusion resistance is the algebraic sum of the separate resistances. 1), 2) and 3) are dependent on stomatal aperture; 3) and 4) are only present in still air.

For a series of stomatal apertures from 0 to 20μ every one of these resistances was calculated and the theoretical transpiration rates for still air and wind calculated accordingly. They were in good harmony with those observed, only a little lower.

In still air the relation between transpiration and stomatal aperture was much the same as found by STÄLFELT (1932) in *Betula pubescens*. In wind, however, transpiration rates were roughly proportional to the stomatal aperture up to the maximum (20μ). At small apertures the curve is steeper, which was explained by the shape of the stomatal pore.

Wind increased the transpiration rate by 300% at maximal stomatal apertures, but

little at small apertures. A pronounced mutual interference was found at great apertures in still air, but none in wind, where the transpiration rate was entirely accounted for by the diffusion resistances in substomatal air spaces and stomatal pores. Mutual interference of pores and the presence of a diffusion resistance in an adhering air layer seem to be identical phenomena.

No indication of incipient drying was found.

Discussion

F. G. GREGORY: It is not quite clear to me what Dr. VAN DEN HONERT means by the "adhering air layer over an evaporating water surface." This is the fourth of the series of consecutive resistances in the diffusion path. Whereas the other components of total resistance can be estimated from the structural dimensions of the leaf, this fourth stage in general cannot be so determined. By using a circular disc of leaf of known diameter the theoretical value of the resistance to diffusion from this disc is known from STEFAN's law, and thus the maximum value of resistance is known and can be used in the calculation of transpiration in still air. Is this the resistance of the "adhering air layer"? In still air the calculated value of transpiration can be compared with 1) experimental values using the leaf disc and 2) the evaporation from a wet paper disc. The second comparison shows the extent to which STEFAN's law holds, and the first the adequacy of the calculated values of the other resistances (stages 1-3). The fourth stage cannot be estimated from theory. The experimental data in wind could be used to estimate the resistance to diffusion away from the leaf disc, and so the length of the equivalent path of equal cross section could be calculated, which I presume is the estimated thickness of the "adhering air layer".

T. H. VAN DEN HONERT: By the "adhering air layer" in still air is meant a hypothetical plane parallel air layer over the evaporating surface, having a thickness corresponding to the diffusion resistance, which is calculated

from the experimentally determined evaporation rate from a full water surface of the same dimensions. Professor GREGORY suggests that its theoretical diffusion resistance (the fourth resistance in the case of leaf transpiration) may be calculated from STEFAN's law. Although this would be more in accordance with the manner in which the other resistances were calculated (i.e. from structural dimensions), it would not be practical, for in no case is air circulation completely absent, and so its actual value will be greatly dependent on the circumstances prevailing. — Professor GREGORY's other suggestion is to infer this fourth resistance from the experimental values of the leaf transpiration itself. This is quite feasible, and we did it, indeed, when explaining the results obtained by SIERP and SEYBOLD, by HUBER and by STÄLFELT. However, in doing so, one takes for granted a theory we wanted to prove. So we preferred to make an independent determination of this external resistance by means of the wet filter paper disc, where it is the only resistance present. The results with leaf discs proved that the external diffusive resistance over a leaf surface was practically the same. This all refers, of course, to "still air".—In wind the external resistance is negligible in comparison to that in the leaf. For in wind the evaporation rate from a wet filter paper is several times greater than the transpiration rate from a leaf, even at the greatest stomatal aperture.—In this "external resistance" we have included the third resistance in the individual vapour cups over the stomata, because this was in better accordance with the experimental data. This point is, however, open to discussion and perhaps the small vapour cups still remain in wind. In any case the fourth stage of resistance was considered to be absent in wind.

O. V. S. HEATH: Were the stomata measured before, after or both before and after the transpiration determinations?

It seems possible that some opening of the stomata due to wilting (especially in wind) may have occurred during the experiments.

This might account for the slight deviation from theory shown by the data.

T. H. VAN DEN HONERT: The stomata were mostly measured immediately after the transpiration determinations. There was no indication of opening or of closing reactions during these measurements up to the 25th stoma. From the 25th to the 30th the average aperture of many determinations showed a slight decrease, so these last values were discarded. A closing reaction might account for the slight discrepancy between theory and experiment, but I think it more probable that the slight divergence found is due to the difficulty in obtaining exact microscopical measurements of the diffusion path and sufficiently exact mathematical approximations of the corresponding diffusion resistances.

G. G. LATIES (Pasadena, Calif.)

An Oxidative, Cyanide Insensitive System in the Chloroplasts of a Higher Plant

When spinach leaves are rapidly frozen with liquid air or solid carbon dioxide, suspensions of such frozen and pulverized tissue exhibit an appreciable gas exchange, with a characteristically high R. Q. of approximately 1.4. Cell free homogenates of fresh leaves show the same type and magnitude of activity. The observed gas exchange is notably different from the respiratory gas exchange of intact tissue, being completely insensitive to 0.01 M KCN. Malonate, iodoacetate, and fluoride, in concentrations which drastically effect the respiration of intact leaves, have little or no effect on the activity of suspensions of frozen or homogenized tissue.

A heat labile component of the above system is particulate in nature, being readily sedimented by centrifugation. Complete sedimentation follows centrifugation for 15 minutes at 20,000 \times g. The apparent substrate for the oxidative reaction remains in the supernatant following centrifugation, and is heat stable. The nature of this substrate has not yet been elucidated. When the supernatant and

precipitate are recombined, full activity of the homogenate is evinced. Neither pyruvate or succinate, nor glucose, in the presence or absence of ATP, Coenzyme I, and Mg^{++} can replace the supernatant in this respect.

Differential centrifugation studies relating the fraction of the total initial chlorophyll content recovered in the precipitate to the fraction of the total initial activity present in the same precipitate, indicate the particles in question to be the chloroplasts and chloroplast fragments. This supposition is borne out by experiments with whole chloroplasts, suspensions of the latter exhibiting no activity until combined with the supernatant.

The enzyme system here described has a comparatively broad pH optimum lying between pH 4.5 and 5.0. This characteristic, together with the lack of response to additions of glycolic acid, distinguishes this enzyme system from the α -hydroxy acid oxidase found in certain plant tissues. The insensitivity to cyanide, on the other hand, precludes its identity with any of the well known copper or iron terminal oxidases.

Whether or not active preparations are obtainable appears to be dependent upon the temperature at which the plants are grown. Preparations from leaves of spinach plants kept at 18° C for two weeks are without activity, whereas similar preparations from leaves of plants kept at 26° C for the same period of time are highly active. The minimum period necessary for this differential response to temperature appears to be shorter than here reported.

Discussion

D. I. ARNON: Results from our own experiments with the respiration-like activity of isolated chloroplasts differ from those of Dr. LATIES, in that we find inhibition from such inhibitors as fluoride, iodoacetamide and dinitrophenol. The inhibition was particularly effective in CO_2 -evolution. Higher concentrations of inhibitors were required to bring about inhibition of O_2 -uptake. It seems very im-

portant therefore in studying the effect of inhibitors on this system to distinguish between the oxidation and the decarboxylation reactions. It is likely that in this subcellular system it will be possible to observe the differential effects of the various inhibitors on the enzyme systems responsible for these two aspects of normal respiration in leaves.

G. G. LATIES: CO_2 -evolution at all stages of fractionation accompanies O_2 -uptake, with approximately similar respiratory quotients. No differential effects of inhibitors on O_2 -uptake and CO_2 -evolution was studied. The main distinction between the chloroplast enzyme system, described by LATIES, and that described by ARNON was with respect to cyanide sensitivity.

L. PLANTEFOL et A. MOYSE (Paris)

Les oxydations cellulaires et la respiration

L'analyse des échanges gazeux, par nos méthodes, d'organismes ou d'organes végétaux divers: Champignons, Mousses, Phanérogames, soumis à des conditions de vie variées, nous a permis de distinguer parmi les oxydations dites respiratoires celles qui correspondent à une nécessité physiologique et celles dont la réalisation peut être sans lien obligatoire avec l'économie cellulaire.

Il convient tout d'abord d'éliminer des oxydations respiratoires ce que l'un de nous a appelé les *oxydations extrinsèques*: lorsqu'un fragment végétal tel qu'un rameau de Mousse a été immergé dans une solution glucosée diluée, il présente une élévation de l'intensité de ses échanges gazeux qui peut être presque doublée. Cette élévation, pour des concentrations faibles, est sensiblement proportionnelle à ces dernières.

Après un lavage de quelques minutes, l'intensité retrouve sa valeur normale.

D'autres substances: glucides solubles, alcool éthylique, acides aminés, acides organiques provoquent le même phénomène.

A ces oxydations, qui intéressent des substances extra-cellulaires, s'opposent les *oxyda-*

tions intrinsèques ou oxydations respiratoires vraies touchant des métabolites intra-cellulaires.

Parmi celles-ci, il en est dont le rythme est directement lié à la concentration dans les liquides cellulaires des métabolites aisément oxydables tels que le glucose, les acides aminés ou organiques.

Ainsi l'intensité respiratoire des feuilles croît avec leur teneur en glucose, tout au moins jusqu'à une certaine limite, sans que le surcroît d'oxydations par rapport à l'intensité normale ait une nécessité fonctionnelle.

Par ce dernier caractère, ces oxydations se rapprochent des oxydations extrinsèques.

Mais il est d'autres oxydations dont l'intervention fonctionnelle est évidente:

1) *Les oxydations complémentaires*: après un séjour en anaérobiose partielle ou totale, un organe végétal replacé en atmosphère ordinaire, présente une intensité respiratoire plus élevée que la normale. Les métabolites provenant des oxydations incomplètes effectuées en anaérobiose sont alors éliminés par oxydation complète.

L'intensité des oxydations complémentaires est en relation avec la pauvreté en O_2 de l'atmosphère anaérobie au contact de laquelle l'organe a préalablement séjourné; puis très rapidement l'intensité des oxydations retrouve sa valeur normale.

Après une carence en aliment azoté, une feuille qui reçoit de l'N sous forme ammoniacale présente un accroissement de son intensité respiratoire, lié à l'élimination des produits (acides organiques probablement) accumulés au cours de la carence.

Les oxydations complémentaires supposent généralement l'existence d'oxydations incomplètes. Avec ces dernières, elles peuvent d'ailleurs jouer un rôle au cours de la physiologie normale (formation et destruction des acides organiques, des amides, aux dépens des glucides ou des protides).

2) Il est enfin possible de préciser la part qui, dans les oxydations respiratoires, est nécessaire à l'entretien protoplasmique, en pre-

nant comme test la stabilité protéique et en étudiant les relations existant entre l'intensité respiratoire et la teneur en protéines des tissus.

Nous l'avons tenté au cours d'études sur la physiologie foliaire.

a) En carence glucidique une proportionnalité directe s'affirme entre ces deux derniers termes, les protéines assurant l'activation catalytique des oxydations et fournissant en même temps l'aliment oxydé (respiration de famine).

b) En présence d'une grande quantité de glucides, une autre proportionnalité se révèle, sur un rythme beaucoup plus élevé, correspondant à une saturation des catalyseurs protéiques en substances oxydables (ce sont les organes les plus riches en protéines qui ont l'intensité respiratoire la plus élevée, indépendamment de leur teneur en glucides).

c) Il existe un minimum d'intensité respiratoire comme il existe un minimum de teneur en glucides pour un organe renfermant une quantité fixe de protéines.

Ce minimum caractérise la *respiration d'entretien*.

La *croissance protoplasmique* ne s'effectue que si les oxydations respiratoires sont supérieures à ce minimum.

The paper was read by M. MOYSE.

J. LEVITT (Columbia, Mo.)

Metal-Protein Complexes in the Potato

A technique was developed for isolating and fractionating the proteins of the potato tuber. Some 40-50 per cent of the extracted protein remained soluble after dialysis. Another 5-10 per cent was soluble in M NaCl. The water soluble fraction was further fractionated by acid precipitation. An increase in the water-soluble components occurred during sprouting but not when sprouting failed to occur under the same environmental conditions (i.e. during the rest period). The acid-precipitated fraction showed an even larger proportional increase.

Fe, Cu, Zn, and Mn were all present in the protein, the first three in about 15 times as high a concentration as in the tuber as a whole. When the pH of extraction and precipitation was varied from 8 to 5, the per cent protein extracted was decreased, the Cu content of the protein slightly increased. Fe and Mn content showed maxima at about 6.5 and 7.0 respectively. The Fe content of the insoluble protein fraction was some 20 times higher than that of the soluble fraction. In the case of the other trace elements the differences were relatively small.

The acid precipitated component of the soluble portion contained much higher concentrations of Fe and Cu than the acid soluble component.

Preliminary results with *Aspergillus niger* revealed even higher quantities of the trace elements in the isolated proteins than in the case of the potato proteins.

Discussion

A. W. GALSTON: I suppose that some metal-containing enzymes may be cleaved into protein plus diffusible prosthetic group by treatment at specific pH's. How then can your pH studies serve to distinguish between "adsorbed" metals and metals which are properly part of the enzyme?

J. LEVITT: The method used was intended to distinguish between metals already chemically attached to the proteins and adsorption of metals not attached to them in the normal cell. This latter might be conceived as occurring at high pH's of extraction, due to precipitation onto the proteins of metals normally in the ionic state.

D. I. ARNON: Re Dr. GALSTON's statement that metals can be dialyzed out of metalloprotein enzymes, it is suggested that it might be desirable to refer specifically to individual enzymes rather than considering metalloprotein enzymes as a group. For example, iron cannot be dialyzed out of hematin enzymes, whereas copper can, under suitable conditions, be dialyzed out of such enzymes as polyphenol-

oxidase or laccase. By referring to each metalloprotein specifically hazardous generalizations can be avoided.

J. LEVITT: Since dialysis was performed in distilled water, no such splitting is to be expected. Certainly, the data do not reveal any.

H. BURSTRÖM: Do you happen to know if your crude protein fractions contain some nucleic acids or nucleoproteids, which are supposed to fix heavy metals?

J. LEVITT: Analyses revealed the presence of P, though in low quantities. Some nucleic acids were therefore probably present, though not very much.

H. BURSTRÖM: Have you obtained any analytical data on fractionating Mn and Fe, which could serve as a background for the discussed mutual interrelation between these two elements?

J. LEVITT: No such data are as yet available.

R. E. GIRTON (Lafayette, Ind.)

Respiration Studies on Excised Maize Roots under Aseptic Conditions

Carbon-dioxide production measurements over periods of 100 hours and longer have been made upon detached, sterile primary roots of germinating hybrid maize grains. The starvation-drift curves thus obtained were characterized by (a) early high, but rapidly declining, rates followed by (b) a period of lesser and slowly-declining rates and (c) a period of still lower rates which again show a somewhat faster decline. No true "senescent hump" was observed in these root starvation-drift curves. During prolonged starvation dry weights and sugar contents decreased considerably. Over the first 50 hours, sugar disappeared more rapidly than could be accounted for by the CO₂ production. The reverse was true for the second 50-hour period. Reducing sugars were initially more abundant than sucrose in these root tissues and disappeared more rapidly during starvation.

Additions of glucose and sucrose to the root medium both gave markedly increased rates of CO_2 production. This was particularly true when nitrates were present and was paralleled by the production of lateral roots. The respiratory rates of sugar-fed roots at 100 hours were approximately four times those of the controls.

The influence of certain respiratory inhibitors on the O_2 consumption of these roots was also studied. Both cyanide and azide resulted in rapid and marked inhibitions of res-

piration. Using M/1000 concentrations, 50% and 40% inhibitions respectively were obtained followed by apparent recovery. The copper inhibitor potassium ethyl xanthate in M/1000 concentration produced no inhibition even when a second addition was made. An iron inhibitor, o-phenanthroline, however, at M/1000 concentration produced a gradually increasing inhibition amounting to approximately 75% in 19 hours. This effect was obtained at both pH 5.8 and pH 7.6.

The paper was read by Mrs. G. M. JAMES.

SESSION 6

July 18th, 9 a. m. — noon

Chairman: A. FREY-WYSSLING

SUBJECT:

Respiration, Salt Absorption

D. R. GODDARD (Philadelphia, Pa.)

Terminal Oxidases and Plant Respiration

Plant respiration involves the oxidation of metabolites with the transfer of electrons through a series of respiratory enzymes (and coenzymes or biocatalysts) to molecular oxygen, with the formation of water and organic acids. These acids undergo decarboxylation, or condensation, with a stepwise oxidation and decarboxylation with the release of CO_2 . In many of the steps there appears to be a compulsory phosphorylation linked with the oxidation.

The nature of the terminal oxidases transferring electrons to molecular oxygen is often unknown. Presumptive evidence of the nature of the terminal oxidase may sometimes be obtained from the action of respiratory inhibitors, such as hydrogen cyanide, hydrogen azide, and carbon monoxide. Light reversal of the carbon monoxide inhibition is strong evidence for the participation of cytochrome oxidase. It has been found that the respiration of embryos and seedlings of peas, barley,

and wheat, and root and immature leaf tissue of carrot, wheat, and barley have their respiration inhibited by 2/3 to 3/4 by low concentrations of cyanide and azide, and photoreversibly by carbon monoxide. However, mature leaf tissue is much less sensitive to these inhibitors.

The presence of cytochrome oxidase has been demonstrated by the activity of extracts of carrot root, pea seedlings, and wheat embryos in the catalytic oxidation of ferro cytochrome c. Cytochrome c itself has been isolated from wheat germ, and by MEEUSE from pea seedlings. The cytochrome oxidase occurs in cell particulates, probably mitochondria. Succinic dehydrogenase accompanies the cytochrome oxidase in the particulates, while ascorbic acid oxidase of pea seedlings is in the supernatant. More than one oxidase occurs in the same tissue, and presumably in the same cell. The potato tuber, long considered a classical polyphenol oxidase plant, contains in particulates a distinct and active cytochrome oxidase; while the pea seedlings contain both cytochrome oxidase and ascorbic acid oxidase,

but no polyphenol oxidase. The absence of cyanide sensitive respiration does not mean that cytochrome oxidase may not be present, for in the fungus *Myrothecium verrucaria*, whose respiration is essentially cyanide resistant, cytochrome oxidase and cytochrome *c* are present. The low level of cytochrome *c* probably indicates that only a small fraction of the total electrons are transferred over the cytochrome system; some as yet unidentified oxidase catalyses the major part of the respiration.

Several distinct oxidases are probably involved in cellular respiration. The results of LUNDEGÅRDH, STENLID, and of ROBERTSON indicate that in roots the absorption of ions is coupled with the cytochrome oxidase system, but that a second oxidase catalyzes the ground respiration. The role of a particular oxidase may not be evaluated only in terms of the percentage of electrons which pass over it, since it may be coupled to a special physiological process. Further, the mere occurrence of an oxidase is not adequate evidence that it functions in normal respiration. The respiratory function of polyphenol oxidase and ascorbic acid oxidase are still not established.

Discussion

D. I. ARNON: I agree with the point of view expressed by professor GODDARD that the demonstration of the presence of an oxidase in the cell does not tell us much directly about its actual function in respiration. Of course an enzyme must first be present to be active, but its mere presence does not define its physiological role. Until the position of a given enzyme is well established in its linkage with the entire chain of enzymatic transformation in a given physiological process there will always be some doubt as to its precise significance in the cell. In this connection it might be well to bear in mind the less frequently discussed properties of individual enzymes. For example, polyphenol oxidase in addition to oxidizing a polyphenol as a substrate can also, as was shown by KUBOWITZ, oxidize re-

duced coenzymes I and II, and in this manner could be linked with the dehydrogenases in the respiration.

H. LUNDEGÅRDH (Uppsala)

The Anion Respiration

The concept "anion respiration" was introduced in 1933. In a series of experiments with roots of wheat seedlings the absorption of neutral salts and the respiration were simultaneously studied. Not only the absorptions of cations and anions of the salt were separately determined but also the quantities of cations given off from the root surface. It was shown that the anions are absorbed in direct relation to a fraction of the total respiration whereas the cations behaved more irregularly. Anions are absorbed in measurable quantities only in the presence of oxygen, whereas cations may be absorbed also under anaerobical conditions, especially in exchange for other cations stored in the roots.

The total aerobic respiration is made up by the ground respiration and the anion respiration. These two groups of processes may also be separated under the influence of certain inhibitors. The ground respiration is not affected by cyanide or azide in concentrations up to 0.001 M or even more, but the anion respiration is completely inhibited by less than 1/10 of this concentration. As newly shown by STENLID α,α -dipyridyl, a specific inhibitor of active iron, also stops the anion respiration, but leaves the ground respiration untouched. The conclusion drawn in the author's laboratory in 1935, involving the identity of the anion respiration system with an enzyme system operating by means of active iron, is consequently well established. At the present stage of biochemical knowledge it is not far-fetched to assume an identity of the anion respiration with the cytochrome-cytochrome-oxidase system.

Before pursuing this biochemical line of thought a few words ought to be said about

the mode of entrance of the salt ions into the surface of the cell. It was experimentally shown that the surface of roots behaves as an amphoteric colloid with dominating acid dissociation. In diluted solutions of neutral salts the surface has a negative potential and the site of this electro-kinetic potential is the protoplasmic membrane of the epidermis cells. The height of the surface potential is determined by the acidity of the membrane and by ion exchange processes occurring between the medium and the membrane. The acidity of the protoplasmic membrane is probably carried by high molecular organic acids the dissociation constant of which, in the case of wheat roots, could be calculated to pK between 1 and 2, thus a comparatively strong acid, probably phosphoric acid in organic linkage. Observations of the surface potential support the assumption of a basic dissociation of the protoplasmic membrane, too, the extension of which, however, is frequently considerably lower than the acid dissociation. The dissociated points of the protoplasmic membrane are apparently arranged in a sparse mosaic in a ground substance of non-dissociated molecules, according to RUHLAND forming an ultra-filter the interstices of which are regulating the entrance of non-dissociated molecules into the cell. Ionized compounds, *e.g.* neutral salts, are severely hampered by their charge and hydration in penetrating the protoplasmic membranes. They are, however, spontaneously attracted by the ionized large molecules in the membrane, a phenomenon to be characterized as an adsorption or more accurately an ion exchange obeying the rule of mass action. At a dominating negative charge of the protoplasmic membrane, as in young roots, cations are most intensively adsorbed. This fact explains the experimentally established ability of extensive non-metabolic absorption and exchange of cations by root systems. Once adsorbed in the protoplasmic membrane the ions are accessible to the interior of the protoplasm by means of repeated exchange processes or rotation of large mole-

cules. An adsorption equilibrium is thus attained between the medium and the *total mass* of the protoplasm of a tissue. In roots of wheat this non-metabolic process is accomplished in less than 12 minutes (at 20° C) after a change of the ionic strength of the medium.

This time course of the non-metabolic absorption and exchange of cations proceeds fast enough to satisfy the demands of salt absorption of the whole plant. But the non-metabolic absorption of anions is too slow for this purpose. It would furthermore be thermodynamically impossible for the cells to accumulate free neutral salts in a higher concentration than in the medium without the expenditure of energy necessary to liberate the adsorbed ions. This energy is supplied by the anion respiration which accelerates the entrance of anions through the surface and accumulates anions in the interior of the cell. The accumulated anions disclose the metallic cations from their places of adsorption in the protoplasm.

Returning to the biochemical mechanism of the anion respiration a theory was developed according to which anions are transported in the opposite direction to the movement of electrons through the cytochrome-cytochrome-oxidase system. Biochemical results bear evidence of a close attachment of some of the cytochromes and of the cytochrome-oxidase to the protoplasmic structure, probably involving a polar structure of the enzyme system itself. If the single components of the system are arranged along an axis perpendicular to the surface of a membrane separating the living substance from the medium, or from the cell sap, anions will inevitably be transported through this membrane. An electron is taken over from the molecular hydrogen, carried by a reduced dehydrogenase as donor, to the first cytochrome, reducing its iron atom from the ferri to the ferro stage. One hydrogen ion is hereby released and dissipated in the surroundings. The electron then passes through the electron ladder formed by the different cytochromes and finally the cytochrome-

oxidase. From here it is handed over to the molecular oxygen. The ionized oxygen joins one hydrogen ion from the surroundings forming water. The activity of H-ions is held constant during the process, because the same quantity is generated at the starting point of the electron ladder. This fact explains why no real transport of cations opposite to the transport of anions occurs in the system despite of the fact that it operates as an electrical microelement. That anions are transported along the ladder in opposite direction to the electrons is a simple consequence of the common rule of electro-neutrality in solutions. I wish once more to call attention to the importance of a polar structure of the operating enzyme system. A disorganized system may continue to carry through oxidation but it has lost its power of real transport of anions.

Arrived at the end of the electron ladder the liberated anions combine with cations in the surroundings, preferably metallic cations which are, as previously mentioned, continuously supplied from the outside according to the predominant cationic adsorption in the protoplasm.

The mechanism pictured transports all kinds of anions according to their activity in the immediate surroundings of the enzyme system and to the mobility of the particles. As the activity of OH- and bicarbonate ions is usually low in the protoplasm, anions of organic acids, *e.g.* malic acid, and of absorbed mineral acids will dominate in the competition. As pointed out by R. N. ROBERTSON theoretically four anions will be transported for each molecule oxygen absorbed. Using slices of storage tissue he was able to observe a quotient very near to 4, if the salts were given in high concentrations. Under similar conditions a maximum value of only about 1 was obtained in roots of wheat, however, according to my recent experiments. These objects show on the other hand a considerable anion respiration in distilled water, thus independently of the active absorption through the surface. This "distilled water respiration" is high immediately

after the transference of the roots from a nutrient solution to aqua destillata but declines to a constant bottom value after the exhaustion of the salt quantities stored in the tissues. The bottom value, on the other hand, is nearly eliminated if the roots are exposed to conditions which have been shown to decrease rapidly the content of malic acid. These experiments, together with extensive observations on the bleeding phenomenon, lead to the following conclusions:

The anion respiration is not restricted to the epidermis of the root only but operates in the bulk of the tissue, transporting stored salts to the stele and probably also transporting organic acids. Even if salts are continuously supplied from the outside the quantities circulating in the tissues are responsible for a considerable fraction of the total anion respiration. It was concluded that under the conditions prevailing in these experiments the total anion respiration of roots exposed to comparatively concentrated salt solutions comprised 25% absorption from the medium, 25% translocation of stored salts and 50% translocation of organic acids.

Even if only ca. 1/4 of the total anion respiration of wheat roots is attributed to active salt absorption, this fraction satisfactorily reflects the quantitative relation between respiration and transport of anions. In one series of experiments the respiration was only partly inhibited by low concentrations of cyanide. It was shown that the absorption of chloride ions was inhibited to the same degree as the respiration, leaving the quotient an/O_2 ($Q \text{ an/O}_2 = \text{absorbed anions/consumed oxygen}$) unchanged. Recently STENLID obtained similar results with α, α -dipyridyl, a specific inhibitor of active iron. Also carbon monoxide inhibits the anion respiration and the absorption of chloride to approximately the same degree. The inhibition of both proceedings is furthermore reversed by illumination with more than 5000 candles white light, as was newly shown in my laboratory by Dr. ERIKA SUTTER. The quotient $Q \text{ an/O}_2$ finally holds fairly constant

during the gradual reversal of the inhibition by cyanide and azide at prolonged treatment with these inhibitors.

All these experiments strongly support one of the fundamentals of the theory of anion respiration, namely the quantitative relation between the absorbed anions and the consumed oxygen. The second fundamental of the theory, namely the cooperation of active iron, is supported by the mentioned biochemical criterions: very high sensitivity to cyanide and azide, complete inhibition by low concentrations of α, α -dipyridyl, complete inhibition by carbon monoxide and reversal of the inhibition by light. A third fundamental of the theory, namely the spectroscopical identification of cytochromes in different stages of oxydation or reduction, has just been attacked in my private laboratory at Penningby. The investigations are only in the beginning but I think it would be of some interest to present a few preliminary results.

Recent biochemical work by GODDARD and others have convincingly shown the presence of cytochrome c and cytochrome-oxidase in higher plants. Hitherto roots were not investigated, however. I have built an apparatus recording the absorption spectrum of living roots of wheat and corn. It comprises a monochromator throwing a small beam of light on a bundle of roots, a photomultiplier cell as receiver, a recording millivoltmeter (Speedomax), and an electromagnetic device moving the wavelength drum of the monochromator synchronously with the Speedomax instrument. The roots are enclosed in a narrow tube enabling a continuous flow of the medium. Wheat and corn give similar spectrograms, showing a uniformly increasing light absorption from about 580 $m\mu$ to ultraviolet and weak bands in the regions 520 $m\mu$ and between 540 and 565 $m\mu$, corresponding to well known bands in the spectrum of cytochrome c. The γ -bands of cytochrome c and $a + a_3$ are also recognized.

Of special interest are the changes in the absorption spectrum induced at exposure of

the roots to different media. At reduction of cytochrome c the γ -band moves from ca. 406 to ca. 416 $m\mu$, and the calculated ox/red-spectrum, *viz.* the extinction of the reduced form minus the extinction of the oxidized form, shows a peak at 418-420 $m\mu$. It was shown that this band is higher in distilled water than in the presence of neutral salts, indicating a rise of the oxidation level of the cytochrome system in the presence of salts.

As to the occurrence of the anion respiration, its presence in roots and in storage tissue of various plants is an established fact. It is to be expected that the system operates preferably on places where an active accumulation against the osmotic gradient is required. A similar system is obviously operating in the gastric mucosa of animals, according to research work performed in the laboratory of Professor KRÆBS in Sheffield. The mere presence of hemin enzymes is of course no proof of the presence of an anion respiration mechanism. It was previously emphasized, too, that an effective transport work postulates not only a polar structure of the body of the enzyme system itself but also an intimate cooperation with the protoplasmic membranes, both perhaps together forming a structural unit. If this unit or this polar structure are disturbed or even damaged some biochemical processes may undoubtedly continue, but the power of salt accumulation is more or less lost. This viewpoint is important in evaluating some recent results with inhibitors apparently disturbing the normal structure of the cell, as 2,4-dinitrophenol. I think Miss WILKINS will make us acquainted, in the following communication, with the effects of such disorders on the transport of salts.

Roots are extremely useful objects of studies on active salt transport because the accumulation mechanism is here overdimensioned to a degree far exceeding the own requirements of the absorbing tissue. The superimposed quantities are exuded in the stele and form the ascending active sap stream, appearing as bleeding from cut roots. My recent

investigations as to the origin of this sap stream and its relation to the anion respiration have shown that the anion respiration conveys an active salt stream through the epidermis of the whole lower part of the root, in the case of roots of wheat seedlings comprising a zone of at least 100 mm length. The stream has a pronounced centripetal direction and is the only polar process in the whole proceeding. The anion respiration stores salt in the cortex cells, but no appreciable movement in a longitudinal direction was observed in the cortex. The sap stream is almost exclusively confined to the stelar vessels and the motive power is a continuous salt exudation from the surrounding living tissue which may be characterized as a vascular epithelium. This internal exudation is independent of any known metabolic process, it is not affected by inhibitors of aerobic or anaerobic respiration. Whereas the anion respiration is continuously filling the salt magazines as long as salts are accessible in the medium, the constant salt leakage from the vascular epithelium represents the down-hill side and the momentary concentration level of the cortex, the steady state. The polar structure of the epidermis, especially its outer protoplasmic membranes, forms a barrier against heavier losses of salts.

As mentioned, water is constantly accompanying the exuded salts. This is a simple consequence of the osmotic conditions prevailing at salt exudation. But besides of these quantities also extra water is given off to the vessels. The extra water is liberated from living cells in which osmotically active material disappears owing to synthetical processes. It was shown that these processes are preferably localized in the tip zone and are sensitive to inhibitors of glycolysis (fluoride).

The active part of the ascending sap stream is thus a pressure flow ("Druckströmung" according to MÜNCH). After its entrance in the vessels of the stele the stream has lost its polarity. It flows upwards simply because the vessels are closed at the lower end. Intermediate root segments bleed at both ends. If the upper

end is clamped by means of a pinch-cock the whole quantity comes out at the lower end. Sap is exuded at all levels from the vascular epithelium and the total bleeding of the root is the integral of the total centripetal transport of salts and water.

Discussion

G. LATIES: With respect to the active iron hypothesis, I should like to ask what is the order of cause and effect? That is, if this hypothesis explains the uptake of anions, is it implied, by the same token, that the presence of anions must stimulate respiration? May a small amount of anion present within the cell act catalytically in this process?

H. LUNDEGÅRDH: The presence of movable anions in the surroundings of the cytochrome system is a condition principally of the same effect as the closing of the outer circuit of an electric element: in both cases no electrons are moved in the interior of the system (or element) if the outer circuit is broken. The activity (concentration and mobility) of the anions surrounding the operating cytochrome system consequently regulates the intensity of the respiration. A small amount of anions present within the cell may be said to act catalytically if they are rotating between the stages of the electron ladder formed by the active iron atoms of the different cytochromes. In roots organic acids obviously play a role as mediators of an "idling" of the anion respiration in the absence of salt respiration, what I have called "distilled water respiration".

E. C. WASSINK: As far as I have been able to understand from your paper, you consider respiration as the driving force for the anion uptake. During your lecture I was reflecting about a possible relation between your findings and ours on phosphate uptake in relation to photosynthesis. I should like to hear your opinion about this.—We conceive phosphate uptake as connected with a probable metabolic use. This is reflected a. o. by the fact that, contrary to the case of anion respiration

tion, in our case uptake is not maximal under the conditions which allow maximal photosynthesis (*viz.*, presence of CO_2).

H. LUNDEGÅRDH: The monovalent phosphate ions (H_2PO_4^-) are easily movable and therefore probably transported in the anion respiration mechanism. Just phosphate, however, is involved in so many biochemical processes that it may be transported in other ways, too. Of course, the fact that most cells owing to the cytochrome system are provided with an effective mechanism of active salt transport does not exclude the existence of other active mechanisms, possibly including not only transference of electrons but also variation of dissociations constants, etc.

H. BURSTRÖM: 1) Do you mean to say that the secretion of ions into the vessels is a wholly non-metabolic process depending upon a mere diffusion from living cells into the vessels? I remember that you had earlier experiments indicating a poisoning of the secretion by glycolysis poisons. A mere diffusion must meet a high resistance in the cytoplasmic boundaries. 2) Have you made determinations of the ratio between concentration of one salt in the water and the concentration in the vessels?

H. LUNDEGÅRDH: 1) As far as my experience goes, the exit of salts in the central vessels of the roots is not conducted by metabolic processes. The glycolytic processes are probably more concerned with the output of extra water and thus control the volume of the sap, not so much its salt contents. An important promoter of the non-metabolic movement of salts through the protoplasm membrane is probably ion exchange and sliding of ions along "adsorption tracks". If the process of diffusion is restricted to the crossing of a thin surface membrane only, its limiting effect ought to be comparatively small. 2) The relation between the concentration of one ion in the medium and its concentration in the bleeding sap has been extensively studied and figures are published, *e.g.* in a paper from 1945 (Ark. f. Bot.).

E. D. H. EL-SHISHINY: In his paper, Profes-

sor LUNDEGÅRDH presented data showing that respiration rate is affected by the amount of anion absorbed, the cations appear of no appreciable effect. In this connection I wish to ask Professor LUNDEGÅRDH how he can explain the results obtained by STEWARD and PRESTON 1941, and SAÏD and EL-SHISHINY 1949 and others, showing the depressing effect of Co^{++} on the rate of respiration of discs prepared from various storage organs, in spite of the great increase of anion level inside the cells due to the preferential absorption of anion in certain experiments.

H. LUNDEGÅRDH: The question is not quite clear to me. The causal relation between the active absorption of salts (anions) and the aerobic respiration is an established fact and apparently contradictory observations are usually caused by a partial destruction of the enzymatic mechanism or some other link in the complete process. Temporary uptake or output of ions may of course be caused by variations in the general balance, *e.g.* one-sided production or disappearance of H^+ , anions of organic acids etc.

D. I. ARNON: Is it correct to infer from the anion absorption theory that there can be no cation accumulation within the cell, unless there is a simultaneous accumulation of anions?

H. LUNDEGÅRDH: The ion balance in the cell is of course dominated by the principle of equinormality of the sum of cations and anions. Cations cannot be accumulated, unless the equinormal quantity of anions is produced or imported. As anions of organic acids are abundantly produced as intermediates of the respiration, metallic cations may be absorbed from the medium without a simultaneous absorption of anions. If the organic acids disappear, the cations are normally given off again as shown by ULRICH and BURSTRÖM. Or an equivalent amount of anions are absorbed from the medium. Metallic cations may also be held by means of adsorption, *e.g.* in exchangeable linkage to non-diffusible organic anions. Such anions are metabolically produced.

R. N. ROBERTSON and M. J. WILKINS
(Homebush, N. S. W.)

The Effects of 2,4-Dinitrophenol on Salt Accumulation and Respiration

The inhibitor 2,4-dinitrophenol, which prevents the transfer of energy-rich phosphate from respiration to energy requiring processes, was used in experiments on carrot tissue. It was realized that in living tissue, 2,4-dinitrophenol may affect the accumulation of ions, either directly by inhibiting a step in the accumulation mechanism, involving a phosphorylation, or indirectly by causing some disorganisation of the cell, thus preventing the accumulation mechanism from operating efficiently.

It was found that 2,4-dinitrophenol inhibits salt accumulation; at high concentrations it may even cause leakage of ions from tissue in salt. Leakage of ions from tissue in water is increased by 2,4-dinitrophenol. The respiration of tissue in water and in salt is stimulated by 2,4-dinitrophenol. This stimulated respiration is inhibited by potassium cyanide. It is also inhibited, light-reversibly, by carbon monoxide. It is concluded that if 2,4-dinitrophenol were preventing the transfer of energy-rich phosphate within the tissue, this transfer would be intimately associated with the accumulation.

Some suggestions are made as to how these observations can be reconciled with existing hypotheses connecting respiration with salt accumulation.

The paper was read by Miss WILKINS.

Discussion

F. G. GREGORY: Is the increased respiration found with added 2,4-dinitrophenol (DNP) both in water and in presence of salts reversible when the tissue is removed to pure water? This should show whether "injury effects" are important.

M. WILKINS: Very few experiments have been done to determine the effect on respira-

tion, of transferring tissues from 2,4-dinitrophenol either in water or in salt to pure water or pure salt. However, numerous experiments have been done in which the transfer of tissue from salt plus dinitrophenol to salt alone resulted in a complete reversal of the inhibition of salt accumulation.

G. E. BLACKMAN: In *Lemna* experiments relating growth to varying concentrations of DNP, the reduction in growth rate is related to concentration, but when the treated plants are transferred back to normal culture solutions, the growth rate of the controls is assumed. The same reactions also hold for the respiration of yeast.

D. I. ARNON: Am I correct in understanding that you obtained an increase of respiration in water at all concentrations of DNP?

M. WILKINS: Yes, we obtained an increase of respiration in water at all concentrations of dinitrophenol, which we used, i.e. up to 36 mgm/l.

K. V. THIMANN: 1) May I ask you if the influence of DNP is sensitive to pH, as is its influence on growth in our experiments? If so, is there a possibility that the pH was not the same in the experiments on accumulation and on respiration? 2) Miss WILKINS stated that the increased respiration caused by DNP is mediated by the cytochrome system; could she give us the evidence for that?

M. WILKINS: 1) In most of our accumulation and respiration experiments we did not use buffered solutions. We found that the pH of an unbuffered solution, which was initially between 4.5 and 5.0, then soon rose to the same value as that of the control in salt, which was usually between 5.0 and 6.0. In the few experiments in which we used buffered solutions we found that the influence of DNP on respiration is sensitive to pH; at pH 3.5 there was a marked inhibition of respiration. 2) The increased respiration caused by dinitrophenol is inhibited by cyanide. Mr. WEEKS from the University of Melbourne has shown that it is inhibited by carbon monoxide, the inhibition being light reversible.

W. RUHLAND (Erlangen)

*Zur Ultrafiltertheorie der Permeabilität
nebst Bemerkungen zur Theorie der Narkose*

Die vom Ref. aufgestellte Ultrafiltertheorie (UFTh) besagt im Gegensatz zu den Löslichkeitstheorien (OVERTON u. a.), dass über die Stoffaufnahme in die lebende Zelle lediglich die rein räumlichen Verhältnisse der Porenweite im Plasma einerseits und der Molekülgrösse der gebotenen Stoffe andererseits entscheiden. Neue Versuche wurden mit *Beggiatoa mirabilis* angestellt, welche wegen ihrer besonders wegsamen Poren die Verwendung von Stoffen eines weit grösseren Bereichs der MV gestattet als andre Pflanzenzellen. Sie hat ferner den Vorzug der Anwendung einer schonenden Turgor-Methode zur Ermittlung ihrer Permeabilität, sowie der sofortigen Erkennbarkeit von Schäden, während die allgemeinen Gesetzmässigkeiten ihrer Durchlässigkeit, insbesondere die auffallende Bevorzugung ätherlöslicher (\pm hydrophober) Stoffe die gleichen sind, wie bei andren Pflanzen und Tieren.

Die Objekte wurden mit homologen Alkoholen der gesättigten aliphatischen Reihe (C_1 – C_6) vornarkotisiert. Sodann wurden Anelektrolyte von verschiedenem MV und verschiedener Löslichkeit zusammen mit dem betr. Alkohol (in gleicher Konzentration wie in der Vornarkose) geboten. Es zeigte sich, dass Alkohole mit kurzer C-Kette nur die Aufnahme grossmolekularer Stoffe hemmen. Die Hemmung greift nach Massgabe zunehmender C-Kettenlänge auf immer kleinermolekulare Stoffe über, wobei das Maass ihrer Ätherlöslichkeit keine Rolle spielt.

Es wird in Übereinstimmung mit Narkosetheorien geschlossen, dass die Alkohole in monomolekularem "kondensiertem" Film mit polar-apolar-parallel geordneten Molekülen die Porenwände der Lipidgrenzschicht überziehen und die Poren verengen, ferner, dass die Porenwege der hydrophilen und hydrophoben Stoffe die gleichen sind. Die Eindiffusion der Stoffe wird also durch die "Molekülbürsten" der Alkohole behindert. Der normal viel ra-

schere Import der Hydrophoben ist auf den weit geringeren Energiegehalt der van der WAALS'schen (intermolekularen) Kräfte ihrer hydrophoben Gruppen (Molkohäsion) zurückzuführen, wie BOGEN betont hat. Demgemäss hemmen sie die Diffusion viel weniger als die hydrophilen. Ob bei dieser Importbegünstigung auch noch eine zweidimensionale Wärmebewegung statthat, die von viel erheblicherer Grössenordnung ist als die gewöhnliche Diffusion, könnte möglich erscheinen, wäre aber für die UFTh kaum vom Bedeutung und bleibe dahingestellt.

Discussion

H. ULLRICH: Die im Salzwasser lebenden Organismen dürften infolge verminderter Hydratation sowieso klarere Verhältnisse betreffs der Ultrafilterwirkung bieten. Fragt man nach der Struktur der diese bedingenden Grenzschicht, so wird man nackte Zellen, etwa die Eier von *Cystosira* oder *Fucus* heranziehen. Behandelt man diese mit Trimethyl- bzw. Triäthyleitrat, so kann man feststellen, dass die zunächst glatte Kontur sich tropfig auflöst. Die winzigen Tropfen treten dann zusammen. Schliesslich wird die Grenzschicht bruchsackartig durchbrochen. Daraus kann man schliessen, dass die Grenzschicht aus fibrillären Eiweissmolekülen besteht, etwa nach Art einer Fasergerüst-Struktur im Sinne FREY-WYSSLINGS. Ihr dürften schichtartig die Lipide aufgelagert sein, die sich dann unter der Wirkung der Estermoleküle ablösen und zusammenscharen.

R. COLLANDER: Ich möchte sagen, dass wir uns alle darüber freuen können, dass der einst so schroffe Gegensatz zwischen Ultrafilter- und Lipoidtheorie der Protoplasma-permeabilität nunmehr grösstenteils ausgeglichen worden ist. Haben wir doch soeben von dem Urheber der Ultrafiltertheorie gehört, dass lipoidlösliche Stoffe bis 10.000 mal schneller permeieren können als in Lipiden unlösliche Stoffe derselben Molekülgrösse. Diese auffallende Begünstigung der Permeation lipidlöslicher Stoffe ist ja eben die Grundtat-

sache, von der auch die Lipoidtheorie ausgeht. Wenn gesagt wird, dass es sich bei der Permeation durch die etwa bimolekulare Plasmahaut nicht um eigentliche Lösungserscheinungen handeln kann, sondern bloss um Auswirkungen zwischenmolekularer Kräfte, so ist das zweifellos richtig. Da aber auch die Lö-

sungsprozesse letzten Endes auf zwischenmolekulare Kräfte zurückgehen, so besteht kein grosser Unterschied zwischen der Aussage, dass das Permeationsvermögen in erster Linie von der Lipidlöslichkeit abhängt, und derjenigen, dass sie durch zwischenmolekulare Kräfte bedingt wird.

SESSION 7

July 18th, 1—3 p. m.

Chairman: K. V. THIMANN

SUBJECT:

Nitrogen Metabolism etc.

H. BURSTRÖM (Lund)

Problems in the Assimilation of Nitrate

The inorganic catalysts proposed as regulators of the nitrate assimilation are manganese and molybdenum; and evidences in the literature support the assumption that both may be necessary, although opinions diverge as to their specific functions and their co-operation in the assimilation of nitrate *per se*. There is an equal uncertainty as regards the aerobic or anaerobic nature of the process. The reason is assumed to be the difficulty of separating nitrate assimilation and protein synthesis from the rest of the metabolism, including ion absorption, respiration, and the growth mechanism.

Experiments have been carried out with the aim of isolating physiologically the nitrate assimilation in roots by means of organic acids, specifically interfering in different parts of metabolism and growth.

Di-n-amylacetic acid, obtained from Dr. VELDSTRA, affects roots in such a way that the elongation of epidermis is checked, and this layer is shed off, although the roots in all other respects seem to behave normally. This causes a complete disappearance of the nitrate assimilation, and it is much reduced even before epidermis is destroyed. This inhibition is counteracted by Mn and Fe but not by Mo.

Investigations on the ion absorption in roots lacking functioning epidermis show a much increased absorption with a tendency to equilibrium between an- and cation absorption, which is explained as follows: the external solution flows through the gaps and even narrow slits in epidermis to the interior of the root, and the sole active absorption mechanism at work is that at the inner reductive level, according to the picture of LUNDEGÅRDH. The oxydative, selective phase of the absorption mechanism seems to be located to the epidermis, and there the assimilation of nitrate is also found. In the acid-treated roots the external solution simply flows around this tissue. The Mn-action is explained by an increased activity of the still living but loosening epidermal parts.

Another acid, α (parachlorophenoxy)-isobutyric acid, supplied by Prof. H. ERDTMAN, acts on the elongation process, presumably as an ideal anti-auxin, devoid of all harmful effects in itself. On roots it accelerates the rate of elongation during the second part of the stretching period, which results in increases in lengths of the individual cells and the whole roots by up to 75%. Analyses of the nitrogen fractions of such roots show that the amount of protein-N closely parallels the number of cells formed, which usually is fairly constant, irrespective of the cell size. The same holds

true if elongation is retarded by auxin, so that the cell elongation may vary by more than 100% without changes in the protein synthesis.

It has thus been possible to locate and encircle the assimilation of nitrate and the ensuing formation of protein in roots; it takes place in the surface layer in connection with the aerobic step in the ion absorption, it is regulated by preferably Mn, secondly Fe, but it is separated from the anaerobic part of the absorption process and also from the whole auxin-regulated metabolism and growth mechanism.

Discussion

F. W. WENT: Have you any indications concerning the effect of light on nitrate assimilation?

H. BURSTRÖM: We have, of course, no indications of light interactions on the nitrate assimilation in roots, only in leaves. As to light effects on roots it should be interesting to investigate their tropistic response under the influence of the anti-auxin.

K. V. THIMANN: What effect is exerted by the parachlorophenoxyisobutyric acid on the growth of shoots? Does it act as an anti-auxin there?

H. BURSTRÖM: This problem has not been investigated. Thus, it is perhaps premature to denote the substance as an anti-auxin before we know its action on shoots also in details.

D. I. ARNON: Would you care to give us some comments on the proposal made by STEWARD some years ago that ion accumulation is related to those metabolic activities which are associated with protein synthesis in the cell and the capacity for cell-division?

H. BURSTRÖM: We have no results which necessitate the assumption that there is a causal connection between protein synthesis and ion absorption. Cell divisions and ion absorption are certainly separated.

H. SAID: Have you found the assimilation of nitrate to follow the classical reduction path? Or is the nitrate built up into protein in a way perhaps similar to your finding

in lighted leaves? I found that in discs from radish roots, nitrate may sometimes disappear and be accounted for almost completely by increase in protein or peptide nitrogen. Under certain conditions, particularly in the presence of aspartic acid, nitrate may, at least partly, be reduced and ammonia-N accumulated from such nitrate reduction.

H. BURSTRÖM: We have made the same observation on roots as you have on discs, that nitrate disappears and protein or amino-nitrogen is formed, but we do not know what path the reaction takes. You cannot under ordinary conditions demonstrate for certain any intermediates. That is just one of the main difficulties.

B. ÅBERG: In connection with professor BURSTRÖM's data on the presumed auxin antagonist I should like to report on another substance which seems to act as an effective auxin antagonist in root growth, namely α -(1-naphthylmethylsulfide)-propionic acid (NMSP), obtained from prof. A. FREDGA, Uppsala. In a concentration of 2×10^{-5} M the average effect upon the roots of flax seedlings grown in solution culture is negligible (lower concentrations stimulate the root growth). This same conc. has, however, a very conspicuous effect upon roots inhibited by 2,4-dichlorophenoxyacetic acid (2,4-D), naphthaleneacetic acid or indoleacetic acid, restoring their growth to a level not far from that of control roots. The following relative growth values, representing several experiments with 2,4-D, may serve as an example:

Control	2×10^{-5} M NMSP	10^{-7} M 2,4-D	2×10^{-5} M NMSP + 10^{-7} M 2,4-D
100	95	22	83

For a more detailed account see *Physiologia Plantarum*, Vol. 3, Fasc. 4, 1950.

W. O. JAMES and G. M. JAMES (Oxford) *The Use of Solanaceous Grafts in the Study of Alkaloid Formation*

Experimental grafting of various alkaloid-forming plants on different stocks has been car-

ried out at Oxford by a team of workers for a number of years, and the results have confirmed the suggestion of former workers that normally the main seat of alkaloid formation in these plants is in the root, and that the alkaloids accumulate in the shoot, especially the leaves, after transport in the transpiration stream. Formation of alkaloids is associated with vigorous metabolic activity and accumulation is also in living cells, in the vacuole.

In experiments with very young seedlings tropane alkaloids were found at a very early stage in the root tips of *Datura* spp. but appeared first in the shoot apices of *Atropa belladonna*, and only later in the roots of this species. The alkaloid was first located by precipitation with iodine in potassium iodide solution, and its presence was confirmed by the purple colour of the Vitali reaction. In grafts of *A. belladonna* on tomato no Vitali reaction was given by extracts from any part of the shoot, but an iodine precipitation was obtained in the apices of all buds. The compound giving this precipitation has not yet been isolated or identified; but is unlikely to be a normal tropane alkaloid.

The shoot systems of *Solanum lycopersicum* grafted on *Atropa belladonna* accumulated alkaloids, which were isolated in the form of hyoscyamine picrate; accumulation was mainly in the leaves, but tropane alkaloids were identified in all parts of the shoot except the fruits, in which no trace was detected at any stage. A normal shoot of tomato fed with 1% atropine sulphate solution accumulated alkaloid in all parts of the shoot except the fruit, in which only traces were detected in tissues adjoining the calyx.

Experiments with radio-active phosphorus (P^{34}) showed that when *Atropa belladonna* is grafted on tomato there is a phloem connection formed and normal phloem transport occurs. Approach grafts in which root and shoot systems of both species were allowed to develop showed alkaloid accumulation in tomato roots as well as shoots; presumably phloem translocation had occurred.

When reciprocal grafts of *Atropa belladonna* and *Datura metel* were examined, the shoot systems showed the hyoscyne/hyoscyamine ratios characteristic of the stock species, indicating formation by roots, and translocation in the transpiration stream.

Leaves from grafted scions will easily form roots when planted in damp sand, and in no case was alkaloid found in leaves from scions of *Atropa belladonna* grafted on tomato until roots were formed; after rooting the alkaloid-content of leaves and root systems increased rapidly, with the chief accumulation in the leaf.

The paper was read by Mrs. G. M. JAMES.

Discussion

F. W. WENT: Since tomatoes easily form roots on their stems, is it possible that *Atropa* plants did so when grafted on other stocks?

G. M. JAMES: Scions of tomato grafted on *A. belladonna* and others regularly form roots, but scions of *A. belladonna* on tomato very seldom do. At present Mrs WILSON has some experiments in which she is trying to induce root formation and investigate the results.

K. MÖTHES: 1) Es gibt sicher zwei Wege der Alkaloidtranslokation: im Xylem von Wurzel zum Blatt, im Phloem von Blatt in Frucht oder vegetative Reserveorgane. Pflöpft man Kartoffel auf *Datura* und lässt Kartoffel Knollen bilden, so wandert in diese auch Alkaloid. 2) Werden Tomaten auf Tabak gepfropft, so können Früchte sehr viel Nikotin enthalten. Wenn bei Ref. Tomatenfrüchte auf *Datura* kein Alkaloid haben, so kann es abgebaut sein. Alkaloidabbau ist eine häufige Erscheinung. 3) Ebenso ist die Alkaloid-Ausscheidung sehr häufig. Das Vorkommen des Alkaloids sagt also noch nichts aus über den Stoffwechsel.

G. M. JAMES: The only evidence we have for phloem transport is the double graft, where alkaloid was found in the tomato root. No alkaloid was detected in leaves of any age in *A. belladonna* scions on tomato, except possibly in the bud apices.

S. ALGÉUS (Lund)

Nitrogen Heterotrophy of a Green Alga

Pure cultures of *Scenedesmus obliquus* were grown with aspartic acid, succinamide and asparagine as the source of nitrogen, and the growth, assimilation of nitrogen and eventual ammonia in the solution were determined. In the aspartic acid cultures cell division took place at a low but constant rate for three months. The N-assimilation was also low but constant. The N-content of the individual cell amounted to approximately 6×10^{-10} mg. Ammonia could not be demonstrated in the culture medium. With succinamide the same final cell count was attained as with aspartic acid, viz. 6,000 per mm^3 but the growth was completed already after twenty days. The N-assimilation ceased at the same time as the cell division and the N-content of the individual cell was the same as in the preceding case. Ammonia was present in the nutrient solution throughout the entire experiment. The rate of growth with asparagine was intermediate between the two foregoing. An inhibition in growth took place first after fifty days and therefore the final cell count was higher than in the two preceding experiments, 10,000 per mm^3 . The N-assimilation proceeded similarly to about the fiftieth day when the N-content of the cells amounted to 30×10^{-10} mg per cell. Ammonia was present during the greater part of the experiment.

In agreement with the idea that amido- and amino-N are split off according to different mechanisms the rates of N-utilization also show great differences as illustrated by the following figures which indicate the average amount of nitrogen split off (assimilated N + ammonia-N) by the individual cell in milligram per cell and day:

Aspartic acid	Succinamide	Asparagine
0.2×10^{-12}	3.2×10^{-12}	1.6×10^{-12}

Asparagine resembles succinamide most closely which indicates that the amido-N is the first to be utilized.

The experiments demonstrate that the amido-N in aspartic acid can be utilized with some difficulty. Deamination or transamination probably has a limiting effect on protein synthesis and growth. No inhibitory substances are formed. The amido-N in succinamide is easily utilized with the liberation of ammonia to the solution. A secondary inhibition, probably caused by the intermediary products formed during the deamidation, sets in, however, at an early stage. If the algae are supplied with both amino- and amido-N in the form of asparagine the latter is chiefly utilized. The products formed during the deamidation do not have an inhibitory action for the first fifty days, and, consequently, cell division and protein synthesis can continue unaffected during this period.

Discussion

H. BURSTRÖM: I do not know if it has ever been shown that transamination can take place with aspartic acid. It is assumed that it is so, but that has never been demonstrated.

S. ALGÉUS: The most important amino acids in the transamination process are no doubt glutamic acid and alanine. If other amino acids can be transaminated is still a question.

K. MOTHEES: Es scheint mir sehr schwer zu sein aus Versuchen, die so lange dauern und bei denen die Eiweiss-Synthese so stark vom Wachstum begrenzt ist, auf den Wert einzelner Verbindungen für die Eiweiss-Synthese zu schliessen. Dass die Säureamidgruppe besonders leicht in die Eiweiss-Synthese eingeht, hat vielleicht noch einen anderen Zusammenhang. Vielleicht geht diese energiereiche Gruppe — ohne zunächst zum NH_3 zu werden — in die Synthese der Peptide ein.

S. ALGÉUS: It was the purpose to follow the nitrogen assimilation in growing cultures. It is a well-known fact that all the nitrogen of the cell is determined by KJELDAHL analyses. From this point of view it would have been better to speak of cell nitrogen instead of protein nitrogen.

F. MOEWUS (Heidelberg)

Physiologie und Biochemie der Selbststerilität bei Forsythia

Forsythia intermedia ist selbststeril und heterostyl. Pollen aus Langgriffler-Blüten keimt nur auf den Narben von Kurzgriffler-Blüten, Pollen aus Kurzgriffler-Blüten nur auf den Narben von Langgriffler-Blüten (Kreuzungsfertilität). Pollen aus Kurzgriffler-Blüten enthält einen Keimungshemmstoff, der mit dem Flavonol Rutin (=Quercetin-3-rutinosid) identisch ist, Pollen aus Langgriffler-Blüten ein anderes Flavonol, Quercitrin (=Quercetin-3-rhamnosid). In den Narben der Langgriffler-Blüten ist ein Rutin-spaltendes Ferment vor-

handen, so dass auf diesen Narben nur Rutinhaltiger Pollen aus Kurzgriffler-Blüten zu keimen vermag. In den Narben der Kurzgriffler-Blüten befindet sich ein Quercitrin-spaltendes Ferment, so dass auf diesen Narben nur Quercitrin-haltiger Pollen aus Langgriffler-Blüten keimt.

Selbstungen beider Blütentypen sind steril, weil Keimungshemmstoff und inaktivierendes Ferment nicht zueinander passen. Selbstungen sind jedoch fertil, wenn der hemmstoffhaltige Pollen in Borsäure suspendiert wird. Borsäure inaktiviert den Hemmstoff durch Bildung von Komplexverbindungen. Blütenknospen sind dagegen selbstfertil, weil im Pollen noch kein Hemmstoff vorkommt, sondern nur Quercetin.

SESSION 8

July 19th, 9—11 a. m.

Chairman: F. G. GREGORY

SUBJECT:

Growth Substances

K. V. THIMANN (Cambridge, Mass.)

The Biochemistry of Growth and Inhibition in Isolated Plant Parts

Previous experiments have shown that the growth (cell enlargement only) of sections of *Avena* coleoptiles and *Pisum* internodes can be prevented by a variety of inhibitors of enzyme systems. An attempt has therefore been made to determine what changes in metabolism take place during such inhibition. *Pisum* internode sections in indole-acetic acid 1 mg/l. (without added carbohydrate) were used. Three inhibitors, namely iodoacetate, arsenite and fluoride, were selected and the concentrations of these which reduce the growth to 50 per cent of that of the controls was determined. During growth, the reducing sugar content of the sections was decreased approximately one-third. In presence of the inhibitors, however, it was decreased still

more. This unexpected result could not be due to accelerated metabolic destruction, since the formation of polysaccharide cell wall is decreased by the inhibitors and the rate of respiration is either decreased or unchanged. Study of other constituents revealed that during growth the neutral ether-solubles are decreased but that the inhibitors powerfully prevent this decrease. It is deduced that these substances (fats) are continuously converted to reducing sugars in the sections. In addition, during growth, protein and asparagine are synthesized; this process is also prevented by the inhibitors. Since so many different processes are prevented when growth is prevented it is deduced that the inhibitors act on reactions common to all processes, such as the oxidative metabolism of organic acids. It has been previously demonstrated that succinate, malate and other acids promote the growth of coleoptiles even in presence of sugar.

An alternative explanation of the above findings could be that the metabolic processes are inhibited as a result, rather than a cause, of the inhibited growth. To rule out this possibility growth was inhibited 50 per cent by a sufficient osmotic concentration of salts or mannitol. Such inhibition resulted in no change in the reducing sugar or asparagine. Thus, growth can be prevented either by interfering with the metabolic system or by directly interfering with the uptake of water. One function of the metabolic system must be to cause the uptake of water. A similar study of the uptake of water by slices of potato tissue has shown that this process has much in common with the growth of isolated stem sections. All the inhibitors found effective with growth are effective on water uptake by potato and the agreement is quantitative.

This concept of growth as water uptake mediated by organic acid metabolism focuses attention on possible ways in which auxin could influence such metabolism. A theory of this action was presented.

Discussion

G. LATTES: Is the water respiration as insensitive to the action of the designated inhibitors as is the respiration in the presence of auxin?

K. V. THIMANN: We have made very few experiments using inhibitors in the absence of auxin; as far as I know, the answer is *yes*.

A. W. GALSTON: I should like to ask: 1) In view of the non-inhibition of growth by malonate and of the known inhibition of the succinoxidase system by this reagent, how may one state that oxidative metabolism of the organic acids is involved in growth? 2) You stated that coumarin is an antisolphhydryl reagent. Yet this compound is also referred to as an anti-auxin; which of these statements is the more accurate?

K. V. THIMANN: 1) The term "non-inhibition" is not justified. Malonate does inhibit growth if its concentration is sufficiently high. It will also inhibit at low pH. Similarly with

isolated succinoxidase systems, quite high malonate concentrations are needed for appreciable inhibition. Reagents like arsenite evidently have a far greater affinity for the enzyme than malonate. The same remarks hold for maleic acid, though its hydrazide seems to be a little more effective than the acid. 2) Coumarin can only be called an anti-auxin in the sense that it prevents the action of auxin, not in the sense that it acts competitively with auxin. BONNER and I have published evidence that it reacts with SH groups. Thus, both statements are correct, with limitations, and subject to further analysis.

H. BURSTRÖM: I do not quite understand your conclusion that auxin and inhibitors act on the same metabolic system. According to your experimental results addition of auxin and the ensuing increase in growth are not accompanied by metabolic changes, whereas the inhibitors interfere in carbohydrate, acid and protein metabolism. This would indicate that they act on different points in the growth mechanism.

K. V. THIMANN: An attempt was made in the diagram to indicate that it was possible to act on the same system, but in different ways. The inhibitors, by slowing down the reactions mentioned, at the organic acid stage, reduce the flow of metabolites. The auxin, however, does not act directly on this flow, but on the linkage between it and the water-accumulating system. It is interesting to note, too, that in all cases, except consumption of reducing sugars the addition of auxin does slightly increase the metabolism. Also, in *Pisum*, though not in *Avena* under our conditions, indoleacetic acid (1 mg per liter) increases oxygen consumption, the increase being 15-20%. Auxin action is therefore "accompanied by metabolic changes," though these may not be very large.

F. W. WENT: It seems to me that the time-curve of auxin and inhibitor effects would indicate that even though auxin-treated but inhibited stem sections grow as much as the

controls, that effect is reached in a very different manner.

K. V. THIMANN: That is true. And correspondingly, it is clear that the biochemistry of the inhibited sections is quite different from that of water controls. However, I believe a more detailed study of the time-curves would reveal that they are different for different inhibitors, since their shape depends on the rate at which the inhibiting concentration is reached within the tissue.

H. LUNDEGÅRDH: Are you not inclined to think that a closer observation of the time course of the processes would disclose some of the complexity of the linkages? My own experiments showed a very rapidly appearing primary response, occurring 1-2 minutes after the application of an inhibitor. Probably, the dissociation of the auxin present in the wall or the protoplasmic membrane is very important here too. After 15-20 minutes the inhibitors (as molecules, not ions) have invaded the bulk of the tissue and may change the metabolism, which then again may lead back to processes, occurring in the surface, or, alternatively, influence the cell reproduction.

K. V. THIMANN: That is certainly possible. The large changes in metabolism which I have described result, of course, from the action of the inhibitors exerted over a relatively long time. We do know from observations of protoplasmic streaming, however, that some action like that you describe is exerted within 2 to 3 minutes on coleoptiles. Our methods of measurement do not allow the determination of changes in growth rate over such short intervals. In some respects, it is an advantage to us to work with longer times, since then the effects of variations in the rate of entry of the different substances do not obscure the ultimate effects.

H. TAMIYA: Have you ever tried to apply auxin and anti-auxin substances in various ratios of concentration, in order to test quantitatively whether they act competitively or not?

K. V. THIMANN: Yes. So far I have not found any case in which an excess of auxin

clearly offsets the action of an inhibitor. Frequently the reverse is the case; because the sections are growing more rapidly in the higher auxin concentrations, the effect of the inhibitor is more masked. Therefore, I doubt whether any inhibitor, which we have studied, can be considered as an anti-auxin in the strict sense.

F. CHODAT: Je suggère, pour expliquer le mécanisme de l'action générale des molécules jouissant de la propriété d'auxine, une hypothèse quelque peu différente de celle qui couronne le bel exposé de M. KENNETH THIMANN: les travaux faits à Genève en 1950 par mon élève ED. PONGRATZ, ont montré qu'il est possible de constituer des modèles spécifiques et puissants d'oxydases, en complexant l'ion cuivre par diverses molécules organiques azotées. Dans la mesure où les molécules jouissant de la propriété d'auxine peuvent complexer les traces d'ion cuivre, toujours présentes dans la cellule, elles acquerront un pouvoir oxydasique autonome. Ces complexes, dont nous avons pu vérifier l'effet *in vitro* et *in vivo*, seraient capables d'exalter brusquement les oxydations qui affectent le cycle de Krebs, carrefour des opérations relatives au métabolisme des acides aminés et des matières grasses. On interpréterait du même coup, les caractères oligodynamiques, instantanés et chimiquement peu spécifiques des molécules jouissant de la propriété d'auxine.

E. C. WASSINK: May I ask if you have measured O_2 alone or also the respiratory quotient? I put this question because I wonder whether fermentative metabolism plays any role, since at least part of the inhibitors you used are known to influence the Pasteur-reaction.

K. V. THIMANN: The R. Q. values are exactly as would be expected from the chemical analyses. In auxin alone the R. Q. is distinctly below 1, corresponding to oxidation of both carbohydrates and fats; all those inhibitors raise the value to about 1, corresponding to their prevention of fat metabolism. The extent to which fermentation proceeds at the

same time cannot readily be deduced from these data. There is other evidence, however, that it does go on in these sections (even when floating on the surface), but that it is not linked with growth.

H. VELDSTRA: As to the employment of the term anti-auxins and the study in this domain, also in connection with the remarks made by Dr. GALSTON, I should like to stress the importance of clearly distinguishing the types of antagonism and of using the methods which in the study on metabolite antagonists with microorganisms made it possible to analyze competitive and non-competitive antagonism etc. In my opinion the term anti-auxin should be reserved for those cases where a direct (biochemical) relation between action of auxin and antagonist can be established and not be used for all sorts of compounds by means of which an effect of auxins can (quite unspecifically) be counteracted.

H. VELDSTRA (Amsterdam)

Some Chemical Aspects of Growth Substance Action

In the earlier part of our work concerning the relation between structure and activity with plant growth regulators, from the results obtained by testing compounds in the *pea-test* we deduced that the five requirements for growth substance activity as given by KOEFFLI, THIMANN and WENT could be condensed to two, both implying a certain relation between the lipophilic part (L=ring-system) and hydrophilic part (H=carboxylic group) of the active compound.

A very definite L/H balance is found for maximal active acids in different series of compounds (to be estimated in the model-system of the oleate-coacervate), and furthermore a specific spatial relation between L- and H-groups is required in such a sense that the —COOH group emerges from the plane of the ring-system (→ threedimensional amphipatic structure).

These last-mentioned spatial relations, mainly to be considered now, were derived from the difference found (by means of molecular models according to STUART) between the structure of trans- and cis-cinnamic acid, only the latter acid being physiologically active. In contrast to the trans-form the cis-acid cannot occur in a flat form and the same is valid for the active cis-forms of β -naphthyl (1)-acrylic acid and 1,2,3,4-tetrahydronaphthylidene acetic acid. Ultraviolet absorption spectra of the three pairs of acids gave additional physical evidence for the non-flat structure of the acids active in the pea-test.

This (three-dimensional) asymmetric distribution of L- and H-parts has now been used as a guide to select active compounds from known series or to synthesize acids for which from this point of view activity could be expected.

Of the o-, m- and p-nitrophenoxyacetic acids the o- and p-acids can occur in mesomeric forms, where the oxygen atom is linked by a double bond to the benzene nucleus and the bond indicated by — in $\text{O} = \text{CH}_2\text{COOH}$ must be situated in the plane of the ring-system. As moreover in this form the still possible rotation of the —CH₂COOH side chain is hindered by the —NO₂ group or H-atoms in the ortho-positions to the side chain, the o- and p-nitrophenoxyacetic acids will occur more frequently in a flat form than the m-isomer, as here the side chain is totally free.

We should expect then the highest activity for the m-acid; actually it was found that in the pea-test it is the only active one.

By partial hydrogenation of the inactive α -naphthoic acid to the 1,2,3,4-tetrahydro-derivative the —COOH group emerges from the plane of the ring system and this acid proved to possess a pronounced activity in the pea-test. The racemate obtained in this way was resolved and it turned out that the (—) acid is more active than the (+) acid, its activity equalling that of α -naphthylacetic acid.

Hydrogenation of the nucleus not bearing

the —COOH group (\rightarrow 5,6,7,8-tetrahydro- α -naphthoic acid), not influencing the spatial position of this group, does not lead to an active compound. So here, too, the results are according to expectations.

For 1-phenylcyclopropane-2-carboxylic acid two forms are possible, one bearing the substituents on the same side of the ring system and one with substitution on opposite sides. Two forms are known, of mp 93° and 105°C respectively. We could prove that in this case the lowest melting one represents the trans-form. This acid being totally inactive in the pea-test, the cis-form of mp 105°C proved to possess quite the same activity as cis-cinnamic acid. This latter fact is very interesting as also in other respects the cyclopropane ringsystem resembles a double bond, and so quite comparable spatial structures, arrived at by different means, show equal physiological activity.

Recently Miss BENTLEY has communicated that 2,3,6-trichlorobenzoic acid is active in the avena-test (straight growth) and that the corresponding aldehyde shows high activity too. With the same acid (kindly placed at our disposal by Dr. SEXTON, Manchester) we could confirm this result in the pea-test, the aldehyde was inactive however. As this substituted benzoic acid at first sight does not fit in with the "spatial scheme" for high activity discussed above, we shall have to analyze whether or not this acid really represents a principally different type of active compounds (cf. the discussion with prof. THIMANN).

Trying to answer the question what the special spatial structure (reminding of that of wetting agents of the branched fatty acid type) suggests as to the essence of growth substance action, we at first have thought that this might be found in a regulation of permeability of the protoplasmic membranes. Subsequent investigations (with the aid of oleate coacervate as a model system and the beet-test as biological object) have proved, however, that this hypothesis is no longer tenable

and that the primary activity resides inside the cytoplasm.

Also in connection with the investigations of KLOTZ et al. and of MURRAY LUCK, TERESI et al. concerning the interaction of organic anions with proteins, it is considered now how organic anions of the specific type of growth substances (cf. the importance of an acid hydrophilic group for auxin-activity) might influence protein-systems (enzymes) and it will be tried to locate the site of action in the cytoplasm (differential centrifugation of cell constituents etc.).

Biological studies had led earlier already to the view that growth substance action is in some way or other related to enzymatic activities, mainly considering the possibility that auxins are part of an enzyme.

From the more chemical point of view influencing (regulation) of enzymatic activity (=action on enzymes) seems to be more probable. In our opinion the most recent papers on both sides show a tendency to convergence, however.

In this phase of the attempts to solve the problem of the mechanism of growth substance action close contact between biologists and chemists is considered to be of prime importance for scientific progress in this field.

Discussion

R. L. WEINTRAUB: Dr. VELDSTRA's thesis rests in large measure upon the presence both of lipophilic and of hydrophilic groups in the active substances. There are known, however, a considerable number of compounds of which derivatives, such as amides, hydrazides, anilides, and esters, possess activities appreciably greater than the free acids themselves. How is this to be explained?

H. VELDSTRA: In none of the standard tests for the evaluation of growth substance activity (Avena-test, both curvature and straight growth; pea-test) derivatives of the acids exceed the parent acid as to the physiological activity. The cases referred to by Dr. WEIN-

TRAUB bear upon effects on intact plants or greater part of plants with native auxin present. That in some of these cases a derivative shows a stronger (complex) effect than the free acid, may depend on differences in rate and degree of penetration and distribution of this more neutral derivative as compared with the acid, whereas the ultimate effect is caused by the acid liberated in the cell. There are indications in this direction, as e.g. KÖGL et al. found that the activities of esters of indoleacetic acid in the *Avena*-test run parallel with the ease with which they are hydrolyzed.

CORNELIA A. REINDERS-GOUWENTAK: You were speaking about permeation of the higher dissociated acids. I should like to know whether you are speaking about permeability or about intrability.

H. VELDSTRA: Indeed, when comparing the rate of penetration of different acids into the cell one should speak of intrability. With the effects studied in the beet-test, where both ecto- and endoplasmic membranes play a rôle, permeability enters into the picture.

K. V. THIMANN: 1. I have also been able to confirm Miss BENTLEY's finding that 2,3,6-trichlorobenzoic acid has activity in the pea test; its activity is quite high and close to that of indoleacetic acid. I should like Dr. VELDSTRA to comment on that. With regard to the corresponding aldehyde, we found only very slight and variable activity, and conclude that this is due to conversion to the acid by enzymes in the plant.—2. However, in this compound, halogen atoms are in the 2,6 position and yet it is active. In phenoxy-derivatives, on the other hand, introduction of halogen atoms or of methyl groups in the 2,6 position makes the compound inactive. There are many examples of this and I wonder if Dr. VELDSTRA can explain the difference between the two types of effect.—3. Thirdly I believe there is some doubt whether the amides and esters really act after conversion to the acids. I have made studies with naphthalene acetamide and find that the shape of the concentration-activity curve is quite different

from that of the free acid, while if action were due to hydrolyses to the acid one would expect the same curve, merely shifted in its ordinates. Furthermore the amount of NH_3 released, ought to be readily detected by Nessler reagent, but no trace of NH_3 could be found. In this case at least I conclude that the amide is active *per se*.

H. VELDSTRA: *Ad 1.* In analyzing the unexpectedly high activity of 2,3,6-trichlorobenzoic acid, at first sight considered as a flat molecule without the spatial features, we found to be of importance in other cases, one has to bear in mind that recently through the investigations of HASSEL et al. it has become known that poly-substituted benzenes are not necessarily of a flat structure. Particularly with 1,2,3-substituted benzenes considerable deviations can occur, as e.g. with 1,2,3,5-tetrabromobenzene where the Br-atoms at C_1 , C_2 and C_3 deviate (on alternate sides) from the plane for 15° . Similar effects could be expected for a di-ortho-substituted benzoic acid, and then again we should have the $-\text{COOH}$ group emerging from the plane of the benzene-nucleus. For the moment these are merely suppositions, which are tested now by investigating all possible isomeric trichlorobenzoic acids, both physiologically and by different physical methods. What ever the results may be, in our opinion the analysis of the finding of Miss BENTLEY will procure important indications for the study of growth substance action.—*Ad 2.* Under 1 is indicated how 2,6-substitution in the trichlorobenzoic acid series might be required for physiological activity. As to the opposite effect in the phenoxyacetic acid series, I cannot offer any convincing argument in a definite direction. To arrive at a solution of this problem it will be necessary to compare complete series of isomeric substituted phenoxy derivatives in detail, also by physical methods.—*Ad 3.* Prof. THIMANN's argument for "own" activity of the amide, based on the form of the concentration-activity curve is rather convincing, but in this case by the conversion of acid to amide

the group remains highly hydrophilic and so the relations referred to by Dr. WEINTRAUB are not principally affected. With the esters, however, one gets a shift from a L/H compound to a L-compound (no longer of non-polar/polar structure) which certainly will have a distribution inside the test-object, quite different from that of the parent acid, and in my opinion the data available up till now strongly indicate that the esters are not active *per se*, but only after hydrolysis to the acids.

H. LUNDEGÅRDH: What are your thoughts about the influence of dissociation on the activity (through a change in intramolecular tension)? My experiments indicate a large influence of the dissociation of the auxin molecules on the degree of their activity.

H. VELDSTRA: Differences in spatial structure of isomeric acids, as *e.g.* of *cis*- and *trans*-cinnamic acid, are reflected indeed also in the degree of dissociation of the compounds. By this way differences in spatial structure (intramolecular tension) in principle could influence the physiological activity, which often decreases with increasing dissociation. However, in the cases studied until now it appears that the only active or most active compound of such pairs of acids is the strongest acid. So the relations are the reverse of those one had to expect when the steric factor in physiological action was operating by means of influencing the degree of dissociation.

H. M. DIXON (Dublin)

Mitotic Hormone

A continuous cytoplasmic lining is found in the developing embryo-sac of many seed-plants. In this lining numerous nuclei are more or less uniformly distributed; these nuclei undergo frequent mitoses during the enlargement of the embryo-sac. The successive phases of these mitoses, as long as the lining is a single layer thick, are grouped together in orderly linear sequences. When, however, separating cell-walls are developed, the stages

of mitoses in adjacent cells lack the co-ordination which characterizes the arrangement observable in the nuclei of the continuous protoplasmic film.

These observations seem readily explained by the action of a mitotic hormone diffusing from a centre in the neighbourhood of the micropyle, towards the base of the embryo-sac.

R. WEINTRAUB (Camp Detrick, Frederick, Md.)

Studies on the Action of Exogenous Plant Growth-Regulators

There are now known some hundreds of organic compounds which have the property, in relatively small amounts, of influencing the mode or rate of a variety of growth and developmental processes in plants. Although the generic term "growth-regulators" has been widely employed to embrace such compounds, the majority of which have not as yet been demonstrated to occur naturally in higher plants, it is not clear to what extent the various end effects may be interrelated through common mechanisms of action. The present report deals with the effects of representatives of three of the principal classes of growth-regulatory chemicals, indole-3-acetic acid (IAA), 2,4-dichlorophenoxyacetic acid (2,4-D), and 2,3,5-triiodobenzoic acid (TIBA), upon three physiological processes in *Phaseolus vulgaris*:—stimulation of cell elongation, induction of abscission, and the so-called "formative" repression of leaf expansion.

Cell elongation. Cell elongation in the hypocotyl is stimulated both by IAA and by 2,4-D which therefore fit the definition of auxins. The two compounds together act additively. TIBA alone is without effect on cell elongation but in admixture with either of the active substances produces an antagonistic or a synergistic effect depending upon the ratios employed.

Abscission. Application of TIBA to the terminal bud results in the formation, within a few days, of an abscission layer in the subja-

cent internode. A similar response is induced by excision of the terminal bud. Application of IAA concurrently with the TIBA prevents the abscission-inducing effect of the latter. Of the order of 8 to 10 molecules of IAA per molecule TIBA are required for complete antagonism. The constancy of this ratio with varying doses of TIBA is the type of evidence which has commonly been assumed to signify that the antagonism is of the competitive type, *i.e.*, that the interference is with a reaction in which IAA is a reactant rather than with one in which it is a product.

Formative response.—This effect, which is characterized by production of closely packed, thick-walled, parenchyma-like cells in place of the normal chlorophyllous mesophyll tissue and consequent diminished lateral expansion of the leaf, is a typical response to 2,4-D. It is not produced either by IAA or by TIBA. The formative responses to 2,4-D can be completely prevented by application of IAA. Approximately 100 molecules of IAA are required per molecule of 2,4-D. This ratio appears to be substantially constant, again suggesting an inhibition of the competitive type.

SESSION 9

July 19th, 1—5 p. m.

Chairman: F. G. GREGORY

SUBJECT:

Growth Processes, Photoperiodism

A. W. GALSTON (Pasadena, Calif.)

Riboflavin as a Photoreceptor and its Relation to the Light-Growth Reactions of Plants

Riboflavin (vitamin B₂) is a water-soluble, fluorescent yellow substance found, so far as we know, in all plant cells. Practically nothing is known of its function in plants although it is generally assumed to act as a respiratory carrier. We have gathered considerable evidence which indicates that free riboflavin and certain flavoprotein enzymes may become activated by light, and that reactions carried out by such light-activated flavins are important in phototropism and perhaps in other light-growth reactions of plants.

Our interest in flavins began with the observation that the growth of etiolated pea epicotyl sections in the light was greatly inhibited if traces of riboflavin were added to the medium. This growth inhibition is not manifested in darkness. The mechanism of the effect was found to be a flavin-sensitized photo-

oxidation of the auxin indoleacetic acid (IAA) which was added to the medium. Since the growth of the sections is dependent on auxin, photo-oxidation of IAA leads to a growth inhibition.

The action spectrum for the photodestruction of IAA by a *brei* of etiolated peas was investigated by the use of a large two-prism spectrograph. The spectrum obtained had a peak at 4400 Å, a minimum at 4100 Å and a long wavelength cut-off point at about 5200 Å. It thus corresponds very well with the absorption spectrum for riboflavin, and with the action spectrum for the *in vitro* riboflavin-IAA reaction. These experiments establish riboflavin as the major photoreceptor in the light destruction of auxin in plant cells. Riboflavin will also sensitize the photodestruction of indole-containing compounds, histidine, peptides containing histidine or tryptophane, enzymes and bacteriophages. Other fluorescent pigments can also photosensitize such reactions.

Riboflavin is found in abundance throughout the *Avena* coleoptile, including the very

light-sensitive tip. Riboflavin will sensitize the photodestruction of the diffusible auxin gathered from *Avena* coleoptiles. A carotenoidless mutant of *Zea* shows normal phototropic response. Riboflavin, not carotene, is therefore the photoreceptor for phototropism.

The IAA-oxidase of peas consists of a light-activatable flavoprotein enzyme which produces H_2O_2 plus a peroxidase which utilizes the H_2O_2 for the oxidation of IAA. The light activation results from an enhanced production of H_2O_2 , thus overcoming a natural inhibition imposed by Mn^{++} , which inhibits by decomposing the H_2O_2 produced by the flavoprotein. Evidence has also been obtained for light effects on other flavoprotein enzymes.

Discussion

J. B. THOMAS: Did you carry out any experiments on carotenoid sensitized photoinactivation of indoleacetic acid *in vitro*?

A. W. GALSTON: Yes, we have attempted this experiment, but always with unsuccessful results. I should, however, add that we did not satisfactorily overcome the difficulties of mutual insolubility of carotenoid- and IAA-containing solutions. More experiments in this field are needed.

E. C. WASSINK: When reading SCHURIGER's paper, I got the impression that carotene might not be exclusive in this respect, but that the same reaction might be produced e. g. by chlorophyll, eosin a. o. as well. What is your opinion about this?

A. W. GALSTON: I certainly agree with Dr. WASSINK's remarks. There is nothing magical about riboflavin, since many other fluorescent pigments will act in a similar manner. However, riboflavin is the only pigment existing *in vivo*, which I know to produce the photodynamic effects described in the paper.

F. W. WENT: I would suggest that the two phototropic systems in the *Avena* coleoptile, the tip and the base reaction, depend upon two different light receptor systems: the tip reaction depending upon a carotene, the base reaction upon a riboflavin system.

S. B. HENDRICKS, H. A. BORTHWICK, and M. W. PARKER (Beltsville, Md.)

Action Spectra and Pigment Type for Photoperiodic Control of Plants

Floral initiation of both long and short day plants can be controlled by irradiation near the middle of adequate dark periods. Quantitative measurements of incident radiant energies in various wave length regions required for a given response show that the basic mechanism is the same in the two types of plants. This photoresponsive system also controls leaf elongation and internode response in some dark grown seedlings as well as many other growth phenomena, some of which are not photoperiodic.

Energies required in the region of maximum effectiveness for control of floral initiation are of the order of 10^5 ergs/cm²/treatment and are of the same order of magnitude for an extensive variety of responses including control of reproductive activity in some animals.

The pigment concerned has its maximum absorption near 6400 Å with a minimum in the visible near 4800 Å. The action spectra as measured for control of floral initiation in *Soja max* var. *Biloxi* parallels, within the limit of experimental error, the absorption spectrum of C-Phycocyanin from *Aphanizomenon flos-aquae*. This indicates that the pigment is of an open chain tetra-pyrrole type and that its response is not seriously modified by self screening or absorption due to other leaf pigments. The pigment is present in acarotenoidous albino plants of *Hordeum vulgare* L. in amounts below limits of detection as yet applied, but still biologically effective.

The paper was read by Dr. S. B. HENDRICKS.

CORNELIA A. REINDERS-GOUWENTAK and L. SMEETS (Wageningen)

Substances Involved in Fruit and Flower Drop

Shedding of flowers and young fruits in tomato may be greatly reduced by spraying with

a solution of alpha-naphthylacetic acid (NA). The swelling in the separation zone of the pedicel undergoes anatomical changes (Proc. Kon. Akad. Wet. Amsterdam 51, 1948). The effect of NA and of the growth inhibiting substances coumarin, ferulic acid and caffeic acid has been examined, of the latter two substances as they are naturally occurring in tomato fruits (VELDSTRA, Rec. trav. chim. Pays-Bas 66, 1947; our thanks are due to Dr. VELDSTRA for supplying us with these substances).

NA brings about a larger swelling in not stopped plants only. In stopped plants NA has no effect over the water checks and the swelling is as large or even larger than in the NA treated not stopped plants. So in stopped plants more of the naturally occurring growth hormone seems to be available for the development of the swelling.

Coumarin or ferulic acid has no appreciable inhibiting effect in combination with NA in not stopped plants, but they have in plants which are not allowed to continue their upward growth. Caffeic acid in combination with NA or applied alone seems to have a slightly enhancing effect in not stopped plants; its effect in stopped plants has not yet been examined.

Applied without NA the inhibitors (excepted caffeic acid) have an inhibiting effect on the naturally occurring growth hormone.

The paper was read by Dr. REINDERS-GOUWENTAK.

T. HEMBERG (Stockholm)

The Role of Growth-Inhibiting Substances in the Potato Rest-Period

The rest-period of the potato is not regulated by auxins but rather by growth-inhibiting substances. The auxin content is extremely low during the rest-period and only rises in connection with the germination. Nor is it possible to find any relation between the length of a rest-period and the auxin content. Varieties with a very short or a very long

rest-period may, at that time, contain an extremely small amount of auxin, while the auxin content in varieties with rest-periods of a medium length may be, relatively speaking, considerably higher.

When one-eyed pieces of not resting potato are kept in solutions of indole acetic acid for 24 hours and then planted in sand, concentrations of 10 mg indole acetic acid per litre or more will be seen to inhibit the growth of the sprouts. A solution of 100 mg per litre of indole acetic acid will stop the growth of the sprouts practically completely. On the other hand, lower concentrations, of 0.1–1.0 mg per litre, will not retard the growth but may even stimulate it during periods when the natural auxin content of the potato is low. When one-eyed pieces of resting potato are treated with indole acetic acid, the sprouts fail to show any growth, unless the rest has been broken by an ethylenechlorhydrin treatment.

During the rest-period, a large amount of growth-inhibiting substances is to be found in the potato peelings. As the rest ceases, these substances will largely disappear. When resting potatoes are treated with ethylenechlorhydrin, much of the growth-inhibiting substances will have vanished within 4 days from the initiation of the treatment. Also a glutathione treatment of resting potatoes, which according to GUTHRIE (1940) will break the rest, results in a disappearance of growth-inhibiting substances within an equally long space of time from the beginning of the treatment.

During the rest-period, neutral as well as acid growth-inhibiting substances will be noted in the potato peelings. The amount of neutral substances remains the same during as after the rest-period. An examination of four potato varieties, differing in the length of the rest-periods, disclosed the biggest amount of neutral growth-inhibiting substances in the variety with the shortest rest. Contrariwise, the acid growth-inhibiting substances disappear, as the rest comes to an end, and seem to do so earlier in varieties with short, than in those with long, rest-periods.

Discussion

K. V. THIMANN: Have you any information as to the chemical nature of the growth-inhibiting substances in potato?

T. HEMBERG: I only know that they are acids. I can also say that they cannot be ferulic or caffeic acid. These substances show no inhibiting effect in the *Avena*-test.

K. PAECH: How do the observations of THORNTON (Boyce Thompson Institute) interfere with your observations? He had found that the potatoes are able to sprout as soon as they are put into oxygen-free atmosphere.

T. HEMBERG: Perhaps this treatment leads to the destruction of growth-inhibiting substances.

CORNELIA A. REINDERS-GOUWENTAK: Have you investigated the effect of ferulic acid and caffeic acid in non-decapitated *Avena* coleoptiles? In connection with my own experiments in the tomato-pedicels it would be interesting to get information about the behaviour of the inhibitors in the undecapitated coleoptiles.

T. HEMBERG: No, I have not.

L. BRAUNER: 1) Do you think it is conceivable that the inhibiting substance in potato is indole acetaldehyde?—2) In our experiments the sensitivity of potato tissue to indole acetic acid (permeability reaction) does not change consistently from October to May. What is your experience with seasonal changes of the auxin content in the tissue?

T. HEMBERG: 1) Indole acetaldehyde is according to LARSEN a growth-stimulating and not a growth-inhibiting substance.—2) In the periderm layer the content of acid auxin is low during the rest period and immediately after this period. In the winter the amount slowly rises, attaining a maximum in the spring. This maximum is reached even before the buds begin to elongate noticeably.

R. J. GAUTHERET (Paris)

La nutrition des cultures de tissus végétaux

Certains tissus (Ronce, Carotte) prolifèrent indéfiniment dans un milieu ne contenant que

des sels minéraux, de l'eau et du glucose. La démonstration de ce fait est délicate à fournir car elle exige de recourir à des milieux liquides et à utiliser, pour supporter la colonie tissulaire, un support en ruban de verre. D'autres tissus, très nombreux (Topinambour, Vignevierge, etc.), ont en outre besoin d'une hétéro-auxine. D'autres exigent une hétéro-auxine et en plus de l'acide pantothénique (Aubépine). D'autres enfin (Tabac, *Amorphophallus*) nécessitent une substance de division inconnue présente dans le lait de coco.

Les tissus tumoraux, par exemple ceux de Crown-Gall, prolifèrent indéfiniment dans un milieu ne contenant que des sels minéraux et du glucose même lorsque les tissus normaux correspondants ont besoin de substances de division pour se développer. Ces tissus de Crown-Gall sont insensibles à l'action excitatrice de toutes les substances de division à l'exception de celle contenue dans le lait de coco. Cette dernière stimule considérablement leur développement. En traitant pendant très longtemps des cultures de tissus normaux par une hétéro-auxine on observe une transformation tumorale analogue à celle caractérisant le Crown-Gall.

Les tissus ainsi modifiés sont capables comme ceux de Crown-Gall de se développer en l'absence de facteurs de division même lorsque les tissus normaux correspondants ne possèdent pas cette faculté.

La transformation tumorale, qu'il s'agisse de celle obtenue dans le Crown-Gall ou de celle provoquée par les hétéro-auxines est caractérisée par le fait que les cellules acquièrent un pouvoir exalté de synthétiser des auxines. Dans les deux cas les cellules fournissent des tumeurs par greffage sur des plantes normales. Il existe des degrés très divers dans la transformation tumorale provoquée par les hétéro-auxines.

Les phénomènes de morphogénèse provoqués par les hétéro-auxines sur les cultures de tissus varient selon la dose. A faible concentration (10^{-8}) l'acide indole-acétique stimule la prolifération cellulaire. A dose plus forte (10^{-6})

l'acide indole-acétique devient rhizogène. A dose encore plus élevée (10^{-5} à 10^{-4}) il détermine un accroissement des cellules en tout sens.

L'étude histologique des colonies tissulaires montre qu'à faible dose les phénomènes de prolifération sont accompagnés de la différenciation de formations cribro-vasculaires presque identiques à celle qui caractérisent l'ontogénèse normale. Ces processus d'histogénèse ne dépendent pas de la nature de l'hétéro-auxine employée. Des fortes doses d'hétéro-auxine provoquent au contraire des phénomènes anormaux d'histogénèse dont la nature varie selon la substance.

Discussion

P. NOBÉCOURT: M. GAUTHERET affirme que les tissus de tubercule de Topinambour mûr (en janvier par ex.) sont incapables de proliférer en l'absence d'hétéroauxine. Cependant je présente les photographies de tranches de Topinambour, prélevés en janvier 1940 et qui ont donné de très volumineuses proliférations, en les plaçant simplement sur du coton imbibé d'eau distillée. D'ailleurs, en prélevant les tissus de tubercules de Topinambour à d'autres époques de l'année, on peut également obtenir de volumineuses proliférations de tubercules.

G. MOREL (Cambridge, Mass.)

Recent Advances in Callus Tissue Culture

Plant callus tissue culture is now ten years old. We shall recall briefly how the first results were obtained and we shall comment on the progress made in this field during recent years. The first plant tissue cultures were obtained from various species of dicotyledons. We have shown previously that the tendency to produce calluses of unorganized parenchyma able to be grown *in vitro* seemed to be related to the cambial activity and to the ability to produce secondary tissues. So one could question if callus tissue cultures from plants without secondary bodies, like monocotyledons and vascular cryptogams, were possible.

Our first attempts to solve this problem

were made with monocots producing fleshy organs—certain Araceae (*Amorphophallus* and *Sauromatum*), and also *Gladiolus*. Pieces of tuber from these plants grow very slowly in a mineral solution supplemented with dextrose and auxin. The growth is very much enhanced by the addition of coconut milk to the nutrient medium. Adding this product at a concentration of 15%, we were able to obtain callus tissue cultures of *Amorphophallus* and *Sauromatum* for unlimited periods of time. The tissue of these plants seems to require an unidentified substance present in the coconut milk to proliferate indefinitely *in vitro*.

Our attempts on vascular cryptogams were made from ferns, selaginellas and horse-tails. Since the gametophyte of most of these plants is naturally large and able to grow in an independent manner, we could try to cultivate callus either from the sporophyte or from the gametophyte.

1. *Ferns*. Our main results were obtained with *Osmunda cinnamomea*. When pieces of apical meristem of *Osmunda* are grown in a nutrient medium after destruction of the apical region by needle puncture, they regenerate unorganized calluses. These calluses develop very slowly. They were subcultured several times and kept alive for ten months but finally died. By contrast, calluses appear sometimes spontaneously on the prothallus and it was noticed that they can grow vigorously on mineral solution supplemented with dextrose and a B-vitamin mixture.

2. *Selaginellas*. Pieces from the apical meristem of *Selaginella Willdenowii*, 200 to 500 μ large, grown in nutrient agar, regenerate whole plants, but unorganized callus also appears on the cut surface. These calluses have been subcultured and are growing slowly; as yet we do not know if we will be able to grow them for indefinite periods of time. It is well-known that normally, female gametophytes of *Selaginella* develop very little and die after the development of the sporeling, but megaspores of several species kept in a mineral solution supplemented with dextrose and B-vitamins,

increase several thousand times to form unorganized callus, which can be subcultured indefinitely.

3. *Horse-tails*. Similar results were obtained from nodal pieces of the stem of *Equisetum hiemale*, but not from the gametophyte.

In conclusion we can state that unorganized callus formations which permit tissue culture *in vitro* are not restricted to dicotyledons with cambial activity. When tissue from most of the higher plants is excised and grown on a medium supplemented with proper nutrients, it escapes the regulating influence of the organism and is able to develop calluses of unorganized parenchyma.

Discussion

R. BUVAT: M. MOREL a obtenu des cals, *in vitro*, à partir des cellules du méristème médullaire. Il semble intéressant de remarquer que ces cellules, *histogènes*, ressemblent beaucoup plus, cytologiquement, à des cellules cambiales, également *histogènes*, qu'aux cellules voisines de l'anneau initial, qui sont *organogènes*, et ne semblent pas pouvoir proliférer sans fournir des organes différenciés.

P. CHOUARD: L'un des faits les plus frappants de la communication de M. MOREL est la possibilité de stimuler la croissance des cals ou tumeurs de monocotylédones par le lait de Coco. Voici 14 mois que je conserve, toujours vivants, mais avec une croissance très lente, des tissus de tumeurs épidermiques de feuilles de Liliacées (*Endymion*). J'aimerais entendre quelques précisions de plus sur la composition du milieu qui a permis à M. MOREL d'entretenir la croissance des tissus de cals d'Aracées, et qui pourrait peut-être servir à ces tumeurs d'épiderme.

G. MOREL répondit en donnant la proportion de lait de Coco.

R. J. GAUTHERET ajouta quelques mots sur la distinction entre l'action de l'auxine et celle du lait de Coco.

P. CHOUARD: Les pertinentes remarques de M. GAUTHERET sont corroborées par les observations que j'ai apportées depuis longtemps. Déjà

LAIBACH, puis l'école de KRAUS à Chicago, avait montré que l'auxine stimule la tumorigénèse du cambium et autres tissus proliférants. En 1938, j'ai décrit la possibilité d'obtenir, à partir de feuilles d'*Endymion*, et en fonction de la dose et du temps d'action des auxines, la transformation de l'épiderme, à volonté, en un cal produisant des bulbilles, ou des racines, ou uniquement des tumeurs indifférenciées.

P. A. HENCKEL (Moscow)

The Adaptive Significance of Dormancy in Plants

T. D. LYSENKO who has established a significant relationship between environment and growth and development of plants has shown that dormancy is a very useful biologic adaptation for the endurance of unfavourable external conditions. During the dormancy period a plant is to a certain extent isolated from the surrounding environment owing to an insignificant permeability for water and oxygen because of the presence of the cuticles and cork tissues in branches and buds of the plants.

During our studies in this direction we succeeded in establishing certain characteristic features of the state of protoplasm in plants during the rest period.

In autumn the plants accumulate a considerable amount of hydrophobic colloids particularly fats and lipoids which accumulate on the surface of the protoplasm and the vacuols and a certain dehydration of the protoplasm occurs. During this process the plasmodesms are drawn in by the cell protoplasm and the protoplasm loses its contact with the walls of the cell. We call this process the process of isolation of the protoplasm. In such a state the protoplasm swells but little in the water and does not get injured by the ice crystals in the intercellular spaces. From our point of view this process forms the basis of the second phase of the hardening process of the plant in respect of frost according to TOUMANOV.

Evidence of the presence of a process of isolation is obtained from the following facts:

1. Visual picture of living preparations;
2. Visual picture of preparations fixed by the Flemming solution;
3. Absence of plasmodesms;
4. Shape of the plasmolysis in the sucrose solution (convex plasmolysis).

Apart from this the possibility of determining at that time the osmotic pressure by the plasmometric method as well as the absence of the isolation process in winter type cereals that have passed the yarovization stage and which, as it is known, sharply drop their frost resistance and easily perish even from moderate frosts. In the seeds where the lipid layers are less developed than those in buds and branches the process of swelling in water proceeds with greater rapidity.

The seeds of poplar and willow trees which easily lose their germination power in contrast to other seeds do not possess a process of isolation and during withering their protoplasm is mechanically injured.

During the termination of the rest period it is necessary to destroy the lipid layers and to reestablish the capability of the protoplasm to swell. During the termination of the rest period in branches of woody species by means of warm baths and that of the potato tubers by means of ethylene-chlorhydrin there occurs a destruction of the lipid layers, swelling of the protoplasm, and an increased activity of the ferments.

Apart from the process of isolation of the protoplasm during the rest period under the influence of low temperatures biochemical processes occur which provide for a future normal growth of plants.

While we do not consider that the withering of the plants is exclusively connected with the process of isolation of the protoplasm, we nevertheless attribute to it the leading role in the adaptation of a plant to unfavourable winter conditions.

Discussion

A. VEGIS: Die Resultate, die Professor HENCKEL und seine Mitarbeiter erhalten ha-

ben, stimmen sehr gut mit den Tatsachen überein, die ich früher beim Frühlertreiben der Winterknospen von *Hydrocharis morsus ranae* (1932) und *Stratiotes aloides* (1935) bei Anwendung verschieden temperierter Heisswasserbäder feststellen konnte. Die dabei beobachteten thermischen Koeffizienten Q_{10} waren sehr hoch, ca. 60, was auf eine Auflösung der Fette oder Denaturierung der Eiweiss-Stoffe hinwies.

K. MOTHES: 1) Lipoid-Anhäufung in Zellen, die in einen Ruhezustand übergehen, ist eine sehr allgemeine Erscheinung. Dabei handelt es sich nicht allein um eine lipide Entmischung, sondern um eine absolute Vermehrung der Lipide. — 2) Ich würde diese Substanzen nicht „hydrophobe Kolloide“ nennen. Wahrscheinlich sind sie kleinmolekular und entfalten dadurch besonders leicht eine grosse Oberflächenaktivität. — 3) Auch ich würde den Plasmodesmen eine grosse Bedeutung zusprechen, und ich könnte mir sehr wohl vorstellen, dass eine Anreicherung besonders hydrophober Lipide ihre Einbeziehung verursacht.

H. ULLRICH: Bei reifenden bzw. keimenden Samen von *Soja* oder *Lupinus* zeigt sich, dass die Benetzbarkeit mit fettem Öl für freigelegte Protoplasten bei einer offenbar ganz bestimmten Hydratur sich sprunghaft ändert. Sie ist im reifen, dormanten Zustand sehr gross.

J. LEVITT: Generally, in the case of cortical cells of trees, pits are distinctly visible, and these cells are very favourable for observing plasmodesmata. In hardy cells plasmolysis does not at first reveal Hechtian strands as it does in non-hardy cells. When, however, the hardy cells are very strongly plasmolysed (in 3 M dextrose), the strands appear and can be seen in some cases to join to the pits in adjacent cells. We interpret this as due to a high initial hydration of the hardy protoplasm, its refractive index being the same as that of the surrounding water. They become visible only when dehydrated enough to lower their refractive index markedly.

SESSION 10

July 20th, 9 a. m. — noon

Chairman: E. K. GABRIELSEN

SUBJECT:

Various Papers

H. FITTING (Bonn)

Über die Umkehrung der Polarität bei Laubmoosen

Bekanntlich ist erst in verschwindend wenigen Fällen die Umkehrung der Polarität in Pflanzenorganen geglückt. Die bisher zu wenig beachteten Eigenschaften der Laubmoosprotonemen legen die Vermutung nahe, dass sich unter den niederen Pflanzen die polar gebauten Sporenkeimlinge gewisser Laubmoose für solche Versuche besonders eignen möchten. HEITZ hat (1940/42) ja durch exakte Versuche bewiesen, dass etwa die Sporen von *Funaria hygrometrica* z. B. auf Knopfnähragar (1% Agar + 0,2% Knopfnährlösung) ganz wenige Tage nach der Aussaat mit einem dunkelgrünen, zylindrischen, vorn abgerundeten, stark positiv photo- und negativ geotropischen Chloronema und einem diesem opponierten, nahezu farblosen, dünneren, sich spitzenwärts verjüngenden, negativ photo-, aber positiv geotropischen Rhizoid auskeimen.

Bei allen untersuchten Funarien (*Funaria hygrometrica* Bonner Sippe, *Physcomitrium eurystomum* und *Ph. piriforme*) lässt sich tatsächlich die Polarität ihrer Keimlingschloronemen nach Aussaat der Sporen auf nährstofffreiem 1% Agar (pH=5,5) in typische negativ photo- und positiv geotropische Rhizoide bei jeder Intensität des einseitig einfallenden Tages- oder künstlichen Dauerlichts, aber auch auf Knopfnähragar, sofern dieser das Phosphat als K_2HPO_4 (pH=etwa 7,5) enthält, jedoch nur in stärkerem einseitigem Licht, bei *Funaria* allerdings aus noch unerkannten Ursachen launenhaft, umkehren. Ja, selbst das pH des K_2HPO_4 -haltigen Nähragars (pH=6,2) genügt bei *Funaria* und *Physcomitrium*

eurystomum dazu schon, während die Chloronemen auf solchem bei *Ph. piriforme* sowie auf KH_2PO_4 -haltigem Nähragar nur negativ phototropisch wurden, um sich alsdann sonderbarerweise im Lauf der Zeit, wohl infolge einer Umstimmung durch das helle Licht, wieder positiv phototropisch zu krümmen.

Aber auch die Keimlingsrhizoide wandeln sich besonders leicht auf Nähragar mit KH_2PO_4 (pH=4,85) oder auch noch mit K_2HPO_4 (pH=6,2), ja gelegentlich sogar mit K_3PO_4 (pH=7,5) bei *Funaria*, jedoch nicht bei den beiden *Physcomitrium*-Arten in typische Chloronemen um. Hieraus geht hervor, dass merkwürdigerweise ein und derselbe Nähragar auf die Keimlingschloronemen und -rhizoide ganz verschieden einwirken kann. Wie die Umkehrung der Polarität in den Chloronemen und in den Rhizoiden vor sich geht, liess sich noch nicht ermitteln. Es ist nicht ausgeschlossen, aber nicht beweisbar, dass sie durch eine Umlagerung in den Protoplasten der allein noch wachstumsfähigen reagierenden Endzellen dieser Keimfäden erfolgt. Alle diese Beobachtungen sowie auch das eigenartige phototropische Verhalten der Chloronemen (Umstimmung ihres zunächst positiven in streng transversalen Phototropismus) bei einseitigem Einfall sehr hellen Lichts lassen weitere exakte Untersuchungen sehr wünschenswert erscheinen.

L. BRAUNER (Istanbul)

The Function of the Lamina in the Tropisms of the *Tropaeolum* Leaf

The petioles of cut primary leaves of *Tropaeolum maius*, fixed vertically in the dark, perform an epinastic movement leading after

6 hrs. to a deflection from the vertical of 24.1° . Subsequently this position is approximately maintained. In petioles deprived of their lamina this curvature is reduced to 12.7° . However, if such stalks are supplied from their distal end with 10^{-5} IAA, the reaction rises to 19.1° . This result makes it likely that in the intact leaf the blade acts as a source of auxin for the petiole.

Owing to their epinastism the petioles respond much more strongly to ventral than to dorsal illumination. In intact leaves 3885 lux, applied ventrally, produce in 6 hrs. a phototropic curvature of 85.6° ; applied dorsally, of only 52.7° . Removal of the lamina reduces the ventral reaction to 36.4° ; the dorsal, to 12.2° , i.e. to 42.6% and 23.1% of the corresponding normal curvatures. By supplying decapitated petioles with 10^{-5} IAA their phototropic reactivity can be nearly restored. The respective curvatures thus produced are 76.4° (ventral) and 48.0° (dorsal). Low light intensities (88–547 lux), however, applied dorsally, induce negative phototropism. This effect is probably caused by a photo-turgor reaction. Considering the fact that covering the blade with black paper does not impair the reactivity of the petioles, it can be concluded that the main function of the lamina in the phototropic reaction consists in supplying the stalk with auxin.

Similar conditions also prevail in the geotropism of the leaf. Here again the reaction develops more strongly, if its direction coincides with that of the epinastism. Thus petioles of intact leaves, exposed horizontally with their ventral flank upward (ventral position) rise in 6 hrs. by 40.2° ; from the opposite, dorsal position, by only 29.8° . Removal of the blade diminishes the response in the ventral position by 41.9%, in the dorsal position, by 55.3%. If the decapitated petioles are supplied with 10^{-5} IAA, the curvature from the dorsal position attains 22.0° , thus reaching 73.8% of the corresponding reaction of the intact leaf. In the ventral position the reactivity is increased even more; the curvature

then reaches 52.3° , thus surpassing the normal reaction by 30.1%.

From these observations it can be concluded that in both the epinastic and the tropistic reactions of the *Tropaeolum* leaf the blade serves solely as a source of auxin for the petiole, enabling it to perform growth curvatures. No indication could be found that the lamina acts as a perception organ for the phototropic or the geotropic stimulus. It seems most probable that this function is confined to the petiole itself.

As shown by the figures given above, decapitation diminishes the phototropic reactivity of the petiole considerably more than its geotropic power of response. This is explained by the fact that the mechanism of the phototropic response requires a greater supply of auxin than the geotropic reaction.

Discussion

E. L. NUERNBERGK: 1) Schon vor 1928 hat I. UYLDERT in Utrecht einige Untersuchungen über die autonome Epinastie der *Tradescantia*-Stengel gemacht. Sind die Verhältnisse dort mit denen bei *Tropaeolum* vergleichbar? — 2) Sind Versuche mit dem Abschneiden von Lamina-Teilen gemacht worden, um die Art, wie die Lamina die Auxinverteilung im Stengel regulieren und damit die Richtung der phototropischen Bewegung bestimmen, festzustellen?

L. BRAUNER: 1) Conditions in the stem of *Tradescantia* resemble those in the *Tropaeolum* petiole so far as in both the ventral half is more permeable to auxin. — 2) Removal of one half of the lamina causes curvatures away from the remaining half of the blade.

K. V. THIMANN: Dr. BRAUNER, I understand, ascribes the difference in conduction on ventral and dorsal sides to a difference in the number of bundles. However, if there were a difference in length of parenchyme cells on the two sides, this could have a similar effect. Has he examined the cortical parenchyma?

L. BRAUNER: Apart from the asymmetric distribution of the bundles in the petiole no

anatomic differences were discovered in the tissue. However, a special investigation of this point is still wanting.

P. PREVOT (Paris)

Recherches sur la croissance, la nutrition minérale et le diagnostic foliaire de l'arachide

Les essais plus ou moins empiriques de l'agronomie pratique doivent s'appuyer sur des notions scientifiques aussi précises que possible. C'est ainsi que les recherches sur l'absorption et l'accumulation des ions des écoles de Berkeley et d'Uppsala forment la base d'une meilleure compréhension des échanges ioniques entre la plante et son milieu.

Adoptant ce point de vue, l'Institut de Recherches pour les Huiles et Oléagineux de Paris a fort bien compris que, comme le dit JODIDI (1938), pour l'arachide, «there is a pressing need for exhaustive fundamental studies of the plant in all stages of development and from numerous points of view: anatomical, morphological and genetic, as well as biochemical and biophysical.»

C'est pourquoi, nous avons été chargés en 1948, par cet Institut, d'un ensemble de recherches théoriques sur l'arachide, recherches devant contribuer à élucider certains points d'importance pratique.

Nous avons ainsi été amenés à comparer la croissance, le développement et la nutrition minérale d'une variété d'arachide, la Rose de Loudima, à deux endroits très différents: à Antibes, en France (1948) et à M'Bambey, Sénégal (1949).

Les détails techniques ont déjà été publiés (PREVOT 1949-1950). Nous nous bornerons à donner les résultats principaux dont certains sont inédits.

1) Croissance et nutrition minérale à Antibes (1948)

Les courbes de croissance présentent deux points de changement de pente: un premier à l'apparition des premières fleurs et un second au moment où la plante enfonce de nombreux gynophores dans le sol.

Le début de la floraison «visible» (nous avons en effet montré que l'arachide est sexuée dès la germination) s'accompagne de toute une série de modifications importantes dans la physiologie de la plante: le nombre de feuilles de la tige principale, le nombre de feuilles totales, la longueur des tiges, le poids sec et le pourcentage en eau des feuilles augmentent brusquement. Simultanément, les nodosités radiculaires se développent et forment de nombreuses radicules blanches.

A ce moment aussi les pourcentages en N, K et Ca des feuilles de base de la tige principale s'élèvent.

Le début de la floraison constitue donc un des moments cruciaux dans la vie de l'arachide et ce fait devra retenir tout particulièrement l'attention dans les études d'application d'engrais minéraux à cette plante.

La seconde accélération de croissance qui se produit à l'apparition de gynophores nombreux est en rapport avec l'absorption d'éléments minéraux par les gynophores (voir BURKHART et COLLINS — 1941; THORNTON et BROADBENT — 1948). On constate en effet à ce moment une brusque augmentation dans la vitesse d'accumulation de N et de K par les feuilles basales.

L'analyse séparée des racines, des tiges et des feuilles, met en évidence que les feuilles (spécialement les 5 feuilles basales de la tige principale) — organes d'accumulation — traduisent beaucoup mieux que les tiges (organes de translocation) ou les racines (organes d'absorption) les modifications dans la nutrition minérale de la plante.

Nous confirmons donc les données qui se trouvent à la base du diagnostic foliaire de LAGATU et MAUME et de la Blattanalyse de LUNDEGÅRDH, ainsi que les conclusions de BURKHART et PAGE (1941).

Comparaison de la croissance et de la nutrition minérale à Antibes (France) et à M'Bambey (Sénégal)

A la suite de nos recherches réalisées en 1948 à Antibes, nous avons repris en 1949 cette

étude dans des conditions différentes de sol et de climat au Sénégal.

L'accroissance mesurée en poids frais, poids secs, nombre de feuilles nous a montré que:

1) à M'Bambey, comme à Antibes, il y a brusque accélération de la croissance au début de la floraison, 2) l'allure générale des courbes est la même dans les deux situations, 3) l'intensité de la croissance est différente: le développement foliacé final est beaucoup plus considérable à Antibes.

Par conséquent, l'allure des courbes, c'est à dire la «qualité» des phénomènes correspondant au rythme physiologique de la plante, n'est pas sous la dépendance des facteurs externes.

L'«intensité» des phénomènes est au contraire profondément modifiée par les conditions édaphiques et climatiques.

L'analyse de la nutrition minérale par le diagnostic foliaire (analyse des 5 feuilles basales de la tige principale) permet de déceler de profondes différences entre les deux situations.

On voit en effet que si les pourcentages en azote sont pratiquement les mêmes — ce qui s'explique facilement dans le cas d'une légumineuse, les nutriments phosphorés et potassiques sont déficients à M'Bambey. Pour le calcium, le déficit est spécialement accentué.

Le rôle fondamental du calcium dans le bon remplissage des fruits d'arachide a été bien établi à la suite des recherches réalisées aux Etats-Unis (voir dans GOUNY et PREVOT — 1948).

Nous l'interprétons par une action de mobilisation du Ca sur le N des feuilles. En effet, nous avons trouvé que dans des conditions favorables de croissance, la qualité de la nutrition calcique est l'inverse de la qualité de la nutrition azotée. Le manque de calcium en fin de la végétation à M'Bambey a donc sans doute eu une influence considérable sur la faiblesse des rendements (rendements par pied plus 4 fois plus faibles à M'Bambey qu'à Antibes).

Les résultats que nous avons obtenus sur une variété érigée hâtive, la Rose de Loudima, ne semblent pas spécifiques à cette seule variété.

En effet, à Antibes, nous les avons confirmés sur une autre variété, la Rouge de Loudima.

A M'Bambey, le diagnostic foliaire nous a fourni des indications très semblables pour la Rose de Loudima et la M'Bambey 28206 qui est une variété érigée tardive. Signalons que la courbe de Ca calculée d'après les données de BOUYER (1949) sur une variété rampante est fort comparable aux nôtres.

En résumé, l'étude de la croissance et de la nutrition minérale de l'arachide nous a permis:

1) de mettre en évidence deux époques de la vie de la plante où les phénomènes de croissance et de nutrition sont accélérés:

a) au début de la floraison

b) au moment où la plante enfonce de nombreux gynophores dans le sol.

2) de montrer que des conditions de milieu très différentes, en France et au Sénégal, ne modifient pas le rythme physiologique de la plante, mais ont une profonde répercussion sur l'intensité des phénomènes.

3) de mettre au point pour l'arachide le diagnostic foliaire qui permet de suivre la marche de la nutrition minérale et aussi de déceler les modifications produites dans cette nutrition par l'influence des facteurs externes.

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The paper was read by Mr. M. FERRAND, Paris.

Discussion

C. A. REINDERS-GOUWENTAK: 1) Ce ne sont non seulement les feuilles basales qui fonctionnent, mais je suppose que spécialement après la floraison, ce sont les feuilles *adultes* qu'il faudrait analyser en point de vue des besoins de la plante en relation avec le sol. — 2) La comparaison des *différentes* expériences en s'appuyant sur le pourcentage semble inopportune, le pourcentage lui-même étant un *factum* variable. Je voudrais recommander la surface de la lame comme unité ou — mais ceci en certains cas bien examinés en avant — le poids frais de la feuille.

M. FERRAND: On a demandé si nous n'aurions pas eu des résultats différents en analysant des plantes entières ou toutes les feuilles. — Certainement les résultats auraient été différents mais ils auraient été beaucoup moins exacts. On a montré que les feuilles basales donnaient l'image la plus fidèle de l'absorption des éléments minéraux par l'arachide.

A. CABALLERO LOPÉS (Barcelona)

Relations entre les substances de croissance et la fertilité des plantes supérieures

D'après les récentes données de quelques investigateurs (BURREL et WHITAKER 1939, EYSTER 1941, EMSWELLER et STUART 1948, CABALLERO 1948, WESTER et MARTH 1949) on peut en conclure que les substances de croissance peuvent arriver à vaincre la stérilité de certaines plantes supérieures ou à produire un accroissement sur sa fertilité ordinaire.

Les substances, ainsi que les techniques utilisées à ce but, sont, fondamentalement, les mêmes que pour l'intervention sur les procès

de la fructification: réussite des fruits, parthénocarpie, chute des fruits, etc.

Comme substances actives nous avons employé dans nos expériences: alpha-naphtylacetamide et acide 2,4-dichlorophenoxyacétique. Toutes les deux, bien sous forme de pâte à lanoline ou lanette-wax appliqué directement à des légères érosions faites à la base des ovaires ou sous forme de dissolution aqueuse en pulvérisant les fleurs. Le moment de l'application du traitement doit coïncider, à peu près, avec celui de la pollinisation.

Nous avons réussi à effacer la stérilité sur les plantes suivantes:

Gasteria verrucosa Haw., *G. subverrucosa* Haw., *G. brevifolia* Haw., *G. nigricans* Haw., *G. fasciata* Haw., *G. decipiens* Haw., *G. glabra* Haw., *Aloe zebrina* Bak., *Yucca aloifolia* L., *Agave filifera* Salm.

Ces résultats ont lieu, après autopolinisation, sur des spécimens en culture au Jardin Botanique de Madrid, qui restaient toujours stériles.

Quelques-unes de ces espèces, sous un différent climat, même en Espagne (p.e. au littoral méditerranéenne), sont spontanément fertiles.

Le traitement le plus efficace sur ces Monocotyledones c'est la pulvérisation des fleurs avec une dissolution aqueuse du sel sodique de l'acide 2,4-dichlorophenoxyacétique, concentration vers 1 par mille, au moment de la pollinisation.

Au cas particulier de *Gasteria glabra* Haw. l'étude microscopique des plantes soumises ou non à traitement démontre:

1) Aux plantes non traitées la fécondation et le commencement du développement de l'embryon ont lieu, en apparence, parfois (9%), d'une façon normale, mais toujours l'avortement arrive.

2) Sur les plantes traitées le tant pour cent d'embryons se formant au début s'élève notamment (9 à 63%) et leur avortement est presque annulé (88%).

En vue des résultats obtenus par les différents investigateurs on arrive à la conclusion qu'on trouvera les plus grandes probabili-

tés de succès à effacer la stérilité en cas de autoincompatibilités (EYSTER 1941, EMSWELLER et STUART 1948, CABELLERO 1948) ou bien sur les autogames stériles par manque des conditions climatiques (CABELLERO 1948).

On a obtenu une augmentation de la propre fertilité sur des croisements intraspécifiques (BURREL et WHITAKER 1939, EMSWELLER et STUART 1948, WESTER et MARTH 1949), interspécifiques (EMSWELLER et STUART 1948) et sur des espèces de fertilité pauvre (EYSTER 1941).

Peut-être que le traitement doit son action bienfaisante en provoquant ou stimulant l'afflux des matières nutritives vers l'ovaire en voie de croissance et en empêchant l'action d'inhibition que sur le développement du tube polinique exercent certaines substances spécifiques du pistil.

En ces moments nous sommes en train d'étudier des expériences, déjà réalisées avec un résultat positif, sur Dicotyledones, Cactacées (*Echinopsis* sps.) et Solanacées (*Solanum* sps.).

B. J. LUYET (St. Louis, Mo.)

Ultra Rapid Cooling and the Preservation of Life

The statement that some frozen tissues have a better chance of surviving, if cooling and rewarming have been very slow, is not in conflict with the assertion that a very rapid freezing and thawing sometimes provide the only means for the preservation of life after solidification at low temperature. Both claims are well substantiated, but in different cases or in different conditions. In the work to be summarized here it was found that, when the temperature could be lowered and raised at a rate of some hundred degrees per second, plant tissues could be preserved alive, while they were killed after a slow treatment under otherwise identical conditions. This was obtained with various materials which had a small enough heat capacity to be cooled and rewarmed at the rate mentioned when they were immersed

in liquid nitrogen: for example, layers of epidermis, or moss leaves with their full water content. The physical basis for the interpretation of these results—which is that rapid cooling and rewarming prevent the formation of ice crystals and cause the solidification of water in the amorphous state—will be demonstrated in droplets of aqueous solutions; the methods for measuring and recording ultra-high cooling and rewarming velocities will be described and illustrated; and the application of the method to the preservation of seedlings and of entire higher plants will be discussed.

LELA V. BARTON (Yonkers, N. Y.)

Soaking Injury to Seeds as Affected by Supply of Different Gases

It has been known for some time that seeds of different species of *Phaseolus* are injured by soaking, so that their subsequent germination is impaired. The exclusion of oxygen during the soaking process has been assumed to be detrimental. The present experiments have demonstrated that pure oxygen bubbling through the soaking water increases the injurious effects. Nitrogen or hydrogen supplied during the soaking period reduce the harmful effects somewhat, while carbon dioxide removes them entirely. The deleterious effects of the oxygen have also been apparent after soaking seeds of *Zea Mays*, *Triticum sativum*, *Hordeum vulgare*, *Avena sativa*, *Helianthus annuus*, and *Pisum sativum*, but carbon dioxide did not prevent or remove these effects for all species. Different lines of investigation are being pursued to determine the mechanism of the oxygen action.

Discussion

ANNA MACLEOD: O_2 enhances germination of dormant barley. Have any experiments been carried out with dormant cereals?

L. V. BARTON: We have not tried the effect on germination of dormant grains but the extent of injury by oxygen during soaking is dependent upon the resistance of the seed

coats to water. If seeds do not absorb water easily, they are not so susceptible to injury.

CORNELIA REINDERS-GOUWENTAK: Have you tried to soak the seeds with and without seed coats?

L. V. BARTON: The effect on embryos has been noted and is greater for embryos than intact seeds in *Zea* and *Helianthus* but the reverse is true for *Xanthium*.

R. BOUILLENNE et M. BOUILLENNE-WALRAND (Liège)

La théorie de la rhizogénèse

La proposition de l'hypothèse d'un complexe substantiel déterminant l'organisation des racines, complexe nommé rhizocaline, de nature hormonale, élaboré dans les feuilles, emmagasinées dans les cotylédons et transporté polairement, avait été faite en 1933 par R. BOUILLENNE et F. WENT, sur la base de recherches établies, les unes sur des plantules d'*Impatiens Balsamina* L. et les autres sur des boutures de tiges de *Acalypha Wilkesiana* et *A. Hispida*.

Ces auteurs avaient montré que la néoformation des racines était contrôlée par un facteur (autre que nutritif au sens ordinaire du mot) venant des feuilles et élaboré à la lumière.

Cette hypothèse fut contestée par THIMANN et WENT, lorsque ceux-ci, en 1934, ayant tenté d'isoler la rhizocaline, trouvèrent que la substance extraite était l'hétéroauxine; ils avaient, de plus, constaté que ces auxines extraites ou obtenues par synthèse avaient une action sur la rhizogénèse des boutures. Leurs observations furent largement confirmées. ZIMMERMAN et les collaborateurs de Boyce Thompson Institute montrèrent que non seulement l'acide indol-acétique, mais aussi les homologues et proposèrent une technique féconde concernant le bouturage d'un grand nombre de plantes. Il en est résulté que la nécessité d'un complexe rhizogénique spécifique fut mise en doute par la plupart des auteurs.

R. BOUILLENNE, M. BOUILLENNE-WALRAND

et leurs collaborateurs cependant démontrèrent progressivement, à partir de 1935 que les auxines n'étaient pas facteur rhizogénique en soi et qu'elles restaient inactives dans les cas où un facteur spécifique était limitant. Ils utilisèrent soit des hypocotyles de plantules inanitiées préalablement de manière à constituer un «root-test» permettant de mesurer l'action radicigène des produits d'application, soit des boutures (MOUREAU), soit des cultures d'organes (méristèmes de racines in vitro) (DELARGE).

Dans toutes les expériences réalisées en 1938 avec *Impatiens Balsamina*, il a été mis en évidence par nous que les hypocotyles et épicotyles inanitiés, en présence ou en absence d'hétéroauxine, sont capables de faire apparaître régulièrement un certain nombre constant de racines. Ces racines se forment sur toute la longueur de l'organe pour peu que l'atmosphère de la culture soit humide et pourvue de facteurs alimentaires. Ces mêmes organes non inanitiés en font apparaître davantage.

R. BOUILLENNE et M. BOUILLENNE-WALRAND considèrent ce fait comme très important, car il démontre que l'inanition enlève un facteur rhizogénique mobile venant des cotylédons et réagissant avec l'auxine; mais elle n'en laisse pas moins en place, *tout le long des épicotyles et des épicotyles*, un facteur rhizogénique ne réagissant pas avec les auxines et pouvant initier ce nombre constant de racines (au moins quand le milieu nutritif n'est pas limitant). La mise en évidence d'un facteur rhizogénique fixé, non mobilisable par les auxines et persistant malgré l'inanition, fut bien établie en 1939; elle a été complétée par une étude de la localisation (NOEL) de ce facteur qui se trouve précisément dans les cellules à partir desquelles les racines adventives se forment (péricycle, tissus libériens, cambium). Cette constatation rejoint les faits décrits depuis longtemps en anatomie végétale.

Depuis 1939, beaucoup d'auteurs se sont ralliés à la conclusion que les auxines ne sont pas le facteur essentiellement spécifique de la rhizogénèse et notamment R. GAUTHERET

dans ses belles recherches sur la culture de tissus (1942).

Rassemblant les faits apparemment contradictoires trouvés dans la littérature sur la rhizogénèse et particulièrement confrontant les résultats de l'école de WENT à Pasadena et ceux de Liège, R. et M. BOUILLENNE sont arrivés à une conception du facteur rhizocalinique. Celui-ci est composé d'au moins trois éléments substantiels différents:

1) Un élément mobile, synthétisé dans les feuilles à la lumière, réagissant avec les auxines et qui n'est pas de nature alimentaire. C'est la rhizocaline au sens premier de 1933. La nature chimique de cet élément est actuellement recherchée, ainsi que le lieu de synthèse dans la plante. Un des travailleurs de Liège a montré que l'apparition de cet élément, lié à des radicaux diphénoliques en position ortho, est connecté avec le rôle des poils glandulaires des feuilles à l'état jeune (SIRONVAL, 1948).

2) Les auxines, en concentration biologique, synthétisée également dans les feuilles, circulant éventuellement avec une certaine polarité et pouvant être mises en réserve dans les bourgeons et les graines.

3) La combinaison de l'élément mobile (1) avec les auxines (2) se fait seulement dans certaines cellules (péricyle, tissus libériens, cambium) et nécessite l'intervention d'un facteur de localisation... facteur existant seulement dans les cellules en question et pouvant être de nature enzymatique. La synthèse de ce facteur cellulaire aurait lieu dans les embryons, les méristèmes, les cambiums ou tout autre tissu en voie de multiplication intense. Il serait distribué au cours de la différenciation des tissus par un processus de localisation comparable à ce que l'on trouve au début de l'embryogénèse animale.

La réaction:

élément rhizogénique mobile + auxine + facteur catalytique localisé donne la rhizocaline.

Celle-ci, sous cette forme tripartite, est donc fixée; elle n'est plus sensible à un excès d'auxine; elle n'est plus mobilisable par ces dernières; elle est localisée dans les cellules de

certaines tissus bien déterminés. De plus, cette réaction ne peut avoir lieu que lorsque les trois facteurs sont en présence; c'est-à-dire au prorata de l'arrivée des deux facteurs mobiles dans les cellules qui ont reçu le catalyseur cellulaire, ou qui sont en train de la recevoir au cours de leur division.

La réaction est de plus oxydative, ainsi que l'ont prouvé de nombreuses expériences faites à Liège et dans d'autres laboratoires. L'anaérobiose est restrictive de la rhizogénèse.

Les auteurs précédents considèrent à la suite de diverses expériences entre autres celles de DELARGE (1937) et plus récemment celles de WARDLAW (1947) qu'un ou plusieurs facteurs peuvent être amenés à être déficients ou à manquer et que, dans ces conditions, les cellules nouvelles (méristématiques, par exemple), bien que pourvues des facteurs nutritifs suffisants et capables de proliférer abondamment, deviennent incapables à une différenciation quelconque et se transforment en cals non structurés.

The paper was read by Professor R. BOUILLENNE.

R. DOUIN (Lyon)

Sur le photo-géotropisme des carpophores des Marchantiées

Après avoir observé sur les carpophores du *Marchantia polymorpha* et du *Reboulia hemisphaerica* les différences de sensibilité à la lumière des thalles qui les constituent et mis en évidence la possibilité d'obtenir une pseudo-inversion du géotropisme négatif de ces appareils (1), j'ai déterminé avec précision le degré de la sensibilité à la lumière des carpophores du *Fegatella conica*.

Deux séries d'expériences ont d'abord été faites au cours desquelles les plantes restaient soumises à la fois à la pesanteur et à des éclaircissements continus constants, des témoins étant maintenus à l'obscurité.

Dans la première série d'expériences, les thalles et les carpophores sont disposés en position renversée. Ceux qui sont maintenus à

l'obscurité présentent un géotropisme négatif; les autres, éclairés par en dessous réagissent en fonction de l'intensité de l'éclairement. Sous 5 et 10 lux les pédoncules s'allongent dans la direction de la lumière dont l'action positive annule l'action négative de la pesanteur. Au cours de certaines expériences apparaissent des différences individuelles de sensibilité entre les carpophores.

Dans la deuxième série d'expériences faites dans les mêmes conditions les Fégatelles sont placées de telle façon que les pédoncules soient allongés horizontalement. Les rayons lumineux arrivent par en dessous et tombent perpendiculairement sur les pédoncules. Les observations sont identiques à celles de la série précédente: courbure géotropique négative des pédoncules à l'obscurité et sous des éclairements faibles (10 lux), annulation du géotropisme sous des éclairements plus intenses, différence de sensibilité à la lumière entre les carpophores liée au degré d'élongation du pédoncule et au degré de maturité de l'appareil (sous 12,5 lux les carpophores mûrs à long pédoncule sont géotropiques négatifs, les carpophores à pédoncule court ou assez court sont phototropiques positifs. Enfin la sensibilité des carpophores est spécifique (différence considérable de sensibilité des appareils du *Reboulia* et du *Fegatella*).

Toutefois la sensibilité à la lumière ne peut être exactement déterminée qu'en soustrayant les plantes à l'action de la pesanteur afin d'obtenir une courbure phototropique pure. C'est ce que j'ai réalisé dans une troisième série d'expériences en utilisant un «clino-photostat» construit sur mes données (2). Les Fégatelles soustraites à l'action de la pesanteur sont soumises dans des expériences successives à des éclairements d'intensité décroissante à partir de 10 lux, les rayons lumineux tombant perpendiculairement sur les pédoncules des carpophores. Sous 10, 7, 5, 4, 3, 2 et 1,2 lux, on observe régulièrement une courbure phototropique positive. Dans une dernière expé-

rience, sous 0,5 lux, la courbure se produit encore, mais affecte surtout 2 carpophores plus jeunes que les autres. Cet éclairement de 0,5 lux représente donc approximativement le seuil d'intensité d'éclairement capable de déterminer une réaction phototropique des carpophores dont la sensibilité apparaît très considérable. On conçoit par suite que l'action de la pesanteur puisse être annulée par des éclairements faibles de l'ordre de 12 à 15 lux.

Ces courbures se font par variation de croissance et l'étude anatomique des organes montre que l'allongement plus considérable du pédoncule du côté convexe est en relation directe avec l'élongation plus grande des cellules.

La théorie hormonale des tropismes trouve-t-elle ici son application? Au préalable se trouve la question de savoir s'il existe un centre producteur d'auxines. Si on procède à l'ablation du capitule par sectionnement du pédoncule au sommet, le pédoncule continue à réagir aux excitations phototropiques et géotropiques. Donc, si une auxine intervient, elle doit être élaborée dans toutes les parties du carpophore et notamment dans les cellules du pédoncule. La destruction partielle de l'auxine à la lumière dans les cellules qui la reçoivent directement peut expliquer la courbure, les cellules du côté opposé s'allongeant davantage. Il reste possible qu'à cette action vienne s'en ajouter une autre liée au fait que les cellules sont chlorophylliennes, car MOLLIARD (3) a mis en évidence l'action élongatrice du gaz carbonique intervenant à la manière des auxines.

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SESSION I

July 12th, 1—4 p. m.

Chairman: F. E. FRITSCH, *Recorder:* J. A. NANNFELDT

SUBJECT:

*Taxonomy of Lower Plants with Special Reference to Experimental Methods
(Algae, Lichens, Bryophytes, Pteridophytes)*

E. G. PRINGSHEIM (Cambridge)

The Use of Culture in Algal Taxonomy

The need for cultures in deciding taxonomic problems in the Algae has often been emphasized. Cultures were hoped to provide further features for identification and differentiation supplementing those furnished by mere visual inspection.

A gradual improvement of culture methods, and their adaptation to special requirements has widened the possibilities of application. The main aim has now to be the connection between laboratory and field work. Instances will be given where taxonomical problems have been clarified, or where experimental results call for alteration in taxonomic usage.

KLEBS (1897) "Such [culture] investigations will,--- be of great value in advancing the systematic knowledge of species, not only because they will enable the cycle of forms belonging to a given species to be completely determined, but also because in the diagnosis of the species they will enable new characters to be recognized."

WETTSTEIN (1921) "[Uni-algal] cultures make possible in a much higher degree than the methods hitherto practised the establishment of the degree of variation, thus rendering determinable forms which otherwise could not be identified."

I. General remarks

The need of cultures for answering taxonomic questions in the Algae has often been proclaimed. Cultures were hoped to provide further features of identification and differentiation supplementing mere visual inspection and to prevent confusion of forms living together at the habitat (KLEBS 1897, WETTSTEIN 1921). This demand should not be mistaken as one for bacteria-free cultures which serve different purposes.

A gradual improvement of culture methods and their adaptation to special requirements has widened the range of application. The main aim is now to coordinate laboratory and field work. In the following, instances will be given where taxonomic problems have been brought nearer to their solution, or where experimental results require alterations in taxonomic usage.

There is nothing revolutionary in the results of culture investigations. They are not intended to replace approved methods but to supplement them in providing a firmer basis to morphological descriptions, only rarely adding new features of a more physiological nature. The latter, although worth trying, as CHODAT has shown, did not so far prove as helpful in Algae as in heterotrophic micro-organisms.

Cultures provide information about the taxonomic position of Algae in various ways: 1. material originating from one individual prevents confusion of various species living together at the habitat. An early and well known instance is the separation by KLEBS (1897) of *Botrydium* and *Protosiphon*; 2. the algae can be watched from the beginning to the end of their life cycle, while subsequent samples taken from the habitat often fail to contain the same species again; 3. microscopical investigations can be undertaken repeatedly and at any time, showing often that the organisms are in a healthier state than those collected on excursions; 4. by varying the conditions those factors essential for the species can be found out. Knowledge thus acquired gives a better understanding of its ecological needs. This is important in instances where similar forms are adapted to different surroundings, and ecological conclusions must be revised; 5. alteration of conditions will also bring to light the inherent variability of a species, so that a complete picture of its morphological plasticity becomes available, without which specific diagnoses may be misleading; 6. cultures are useful to establish the connection between early stages and the mature form, to find out whether an alga produces zoospores, is homo- or heterothallic, and so forth; 7. it happened frequently that an alga to be described ceased to be available before all the characters needed to complete the diagnosis had been observed. If it is kept in culture the species can be studied repeatedly and therefore more fully described; 8. one of the greatest advantages, particularly in difficult groups, which often cannot well be preserved, is the possibility to keep in culture

several closely related species so that they can be compared at the same time and under equal conditions. In the *Euglenineae*, *Cryptomonadineae*, many *Chlorococcaceae* and *Volvocales*, and probably also in *Myxophyceae*, this seems to be the only way to improve an unsatisfactory state of affairs, of which many phycologists are conscious. It is only incompletely veiled in our floras and exasperating to beginners.

Laboratory work cannot of course replace field work and is not meant to do so. Culture studies are useful mainly for obtaining better knowledge required for elaborate and reliable descriptions which in consequence facilitate identification. At the same time they show how inadequate our means of doing so still are. Culturing has, however, some drawbacks even for this restricted aim. It takes time to acquire the necessary skill, to prepare media and cultures, and especially to inspect them over and over again. The technique is already simpler now, and the danger of taking artifacts for typical growths is no longer great, particularly if laboratory and field work go parallel as they should.

II. Examples

Everybody will agree that it is difficult or even impossible to identify species of *Euglenineae*. As an example *Trachelomonas* may serve, of which hundreds of species, varieties, and forms have been given names. These are entirely based on the envelopes, mostly without any knowledge of the organisms themselves. A satisfactory picture of the genus and the relationship between its members could not be achieved in this way.

Some fundamental questions of consequence to taxonomy do not seem even to have been asked. What is the significance of varieties and forms in *Trachelomonas*? DEFLANDRE, in his great monograph, is satisfied that they can be recognized by being found in the company of the type. This is a concept different from the definition of the terms in other branches of biology, and it has led to many confusions between reversible modifications and true va-

rieties. Another question, relevant to the taxonomic use of the envelopes and their variability is, whether the shape of the cell-body is determined by the envelope or that of the envelope by the cell-body. A third as yet unanswered question is that for the importance of the colour of the envelopes. Is it characteristic of the species or is it influenced by surrounding conditions? This question cannot be tackled as long as the brown colour is mistakenly attributed to iron compounds. Even the most important question, that for the significance of the cell-body on taxonomy has not yet attracted anybody's attention.

The need of cultures for a detailed taxonomic study of *Trachelomonas* has repeatedly been stressed, but they could not be grown until the soil-water culture technique proved satisfactory also in this instance. By varying the amount and nature of the soil and by adding various substances a better insight was gained, which was then corroborated by pure cultures. The following are some of the results: 1. the more favourable the conditions, the more uniform the population; 2. the formation of the envelopes is in its quality to some extent independent of the multiplication rate of the cells. It is, however, affected by the amount of available iron and manganese in the medium, the latter being responsible for the brown colour of the envelopes; 3. when, in a restricted volume of the medium, iron and manganese or both become deficient by consumption, colour and thickness of the envelopes are reduced so that the state, usually taken as mature, is no longer reached; 4. the same happens in nature where a quick multiplication is followed by a long period without cell-division, and only in the beginning of the former fully developed envelopes are formed, so that a population originates composed of relatively few individuals with elaborate and many with less finished envelopes. The latter may never reach the mature state; 5. to grant the name of varieties and forms to such immature individuals is misleading. They can only have the rank of modifications or status; 6. this does not mean that varieties, i.e. heredi-

tary aberrations, do not exist. Small deviations in envelope shape, ornamentation, shape of collar, etc., were found to be constant in clone cultures. The number of taxonomic forms thus established will, however, be smaller than at present supposed; 7. the naked cell-body is generally more elongate than the encased, and contracts to assume the characteristic shape, previous to excreting the envelope. In some instances, particularly in *Trachelomonas* or *Strombomonas conspersa*, the degree of contraction depends appreciably on conditions, and the various shapes described as so many species seem to be caused in this way; 8. in healthy young cultures the inner structure of the cells is very clear, so that differences, useful in taxonomy, can be observed without staining. They concern the number of chromatophores and especially the structure of the pyrenoids. These are traditionally supposed to be double-sheathed like those of *Euglena gracilis*, but are so only in the aggregate species *Tr. hispida*, while in the majority of the species the pyrenoids are protruding from the inner surface of the chromatophores and covered with a single cap of paramylon, a formation not found in any other genus of the *Euglenineae*. There are no species of *Trachelomonas* without pyrenoids as some authors believe.

In the genus *Euglena* similar questions concerning the bases of taxonomic differentiation can be asked. *Euglena spirogyra* and *E. fusca* are supposed to show differences in several characters, of which only those in dimensions can be confirmed. In this respect, however, they are connected by intermediate forms. Dimensional varieties are found also in other *Euglenaceae* and *Astasiaceae*. Only culture experiments coupled with cytological investigations can decide what their taxonomic significance is.

Unicellular *Volvocales* are almost impossible to identify because newly found forms so often do not correspond with those previously described. This applies to *Dunaliella*, *Polytomella*, *Chlamydomonas*, *Polytoma*, *Carteria*, *Chlorogonium*, *Pteromonas*, and probably other

genera as well. One may be tempted to explain this diversity as the effect of hybridization. But: 1. no sexuality exists in *Polytomella*; 2. colonial *Volvocaceae* are more restricted in their variability than are unicellular *Volvocales*, although they have sexual reproduction; 3. *Euglena*, *Trachelomonas*, and *Menoidium*, which are almost as manifold and difficult to determine, have again no sexual reproduction. Culture experiments, already undertaken at various places, will reveal the cause of diversity.

Still less is known of the definition of species in the *Chlorococcales*, although many of them appear again and again in floristic and ecological papers or have been used for physiological investigations. How far can species of *Chlorella* be recognized by morphological means? Do so-called physiological races occur? In *Ankistrodesmus*, *Scenedesmus*, *Pediastrum*, etc., taxonomic questions have been taken up by various investigators, but with limited success. For general as well as ecological conclusions we should know far more about them, as Prof. THUNMARK has already stated.

Species assigned to *Quadrigula*, *Tetrademus*, *Ankistrodesmus* may possibly be identical, and so may be other colonial and unicellular genera of the *Chlorococcales*, since colony formation is influenced by conditions as WILHELM VI-SCHER has shown. Clone cultures offer the only means to decide these taxonomic questions by subjecting the algae to various circumstances imitating natural conditions.

How many species of *Chaetophora*, *Stigeoclonium*, *Cladophora*, *Tribonema* there are in Europe or even in a more restricted area, nobody can tell, because the distinction between species is inadequate. In all these and many other cases our floras permit at the best only to identify certain forms found in nature and described more or less accurately according to the material available. The splendid way this has often been done, the enormous amount of work involved, or the progress thus achieved I am the last to underestimate, but in many instances our knowledge is grossly incomplete, because the variability and the boundaries of

the species are not established. As long as field phycology is taken as an aim in itself this state of affairs may not require further consideration. When, however, natural relationship is the aim, the life history of the species, including deviations from the so-called type, has to be explored.

A still more complete knowledge of taxonomic units is needed for ecological requirements. Otherwise observations on one form will erroneously be extended to similar but differently adapted forms. In physiology, too, no conformity can be expected between results based on non-identical algal forms, although that has often been done to the great detriment of progress. In the same way as experimenters sometimes refer to *Chlorella* indiscriminately,—results with one of the many physiologically different strains of *Euglena gracilis* have been generalized as covering the whole genus *Euglena*. It sounds unbelievable but it is true that almost every strain of *Euglena* employed in the many physiological investigations bears a wrong name, because the authors did not take the trouble to inspect their material under the microscope and to compare it with the diagnosis of the original author.

The definition of the species of *Chlorella* used in physiological work is not much better. Thus most of the physiological investigations with algae confuse rather than elucidate algal taxonomy. This is a very regrettable state of affairs which is bound to deteriorate further, the more ecologists, physiologists, and biochemists use algae for their purposes as indeed we want them to do. We need therefore a centre of experimental phycology where these problems can adequately be dealt with, and which would provide cultures and advice to those who cannot be expected to find the time for elaborate morphological studies.

W. VISCHER (Basel)

On the Importance of Pure Culture for the Lower Algae

Bark- and stone-algae were taken in pure culture and examined for their systematic re-

lationship and their nutrition. Most of the genera are widespread but cannot be accurately separated into natural categories without pure culture. There is a greater variety than can be seen in observations made in the natural surrounding:

I. *Protococcales Zoosporeae*

1. *Dictyococcus* offers many types which differ through their various kinds of organic nourishment.

II. *Protococcales Autosporeae*

1. *Jaagia* nov. gen. This genus should be distinguished from *Chlorella*. The numerous species are mostly classified under the collective name "*Chlorella ovalis*." Chloroplast somewhat bulky, often with protuberances, with or without pyrenoid; assimilation-product glycogen (?). Autospores unequal in size.

III. *Chaetophorales Leptosireae*

1. *Pleurococcus* NAEGELI (non MENEGLINI). Cell-clusters and short filaments. Chloroplast parietal, with or without pyrenoid.
 - a. Subgenus *Desmococcus*: mostly with pyrenoid; cubic cell-clusters, seldom with short branched filaments. Several species.
 - b. Subgenus *Apatococcus*. Cell-clusters more tetrahedric; no pyrenoid.
 - c. Subgenus *Diplosphaera*. Cubic cell-clusters rare, immediately separating into double-cell groups or single cells; with or without pyrenoid; glycogen.
 - d. Incertae sedis, partly with zoospores.
2. *Pleurastridium* nov. gen. Similar to *Pleurastrum*, but separating into cells, with pyrenoid and starch.

IV. *Prasiolaceae*

Chloroplast star-shaped centrally situated, with large pyrenoid and starch; aplanospores.

1. *Prasiococcus* nov. gen. (*Pleurococcus calcarius* PETERSEN?). Irregular cell-clusters, never filaments.

2. *Prasiolopsis* nov. gen. (*Pleurococcus* MENGH. et auctt.?) Small plants at first with branched filaments, later pseudo-parenchymatic, dividing into cellgroups; aplanospores.
3. *Prasiola* incl. *Schizogonium*.

Beside the species mentioned above many others can be found in the same habitats. *Chlamydomonas*, *Chlorococcum*, *Chlorella*, *Stichococcus*, *Hormidium*, etc., of which precise study is to be made.

Discussion

R. A. LEWIN: Professors PRINGSHEIM and VISCHER have used the terms "species" and "genus"; one might perhaps add a caveat to the use of these terms in algal taxonomy. Changes, of apparently profound taxonomic value, may be produced by what may, perhaps, be single gene changes: thus, "mutations" have been obtained by the use of ultra-violet light, differing considerably from the original forms in culture. One might mention a filamentous form of the usually unicellular *Stichococcus bacillaris*; or wholly palmelloid types, or types lacking flagella, which have been induced in *Chlamydomonas Moewusii*. Without knowledge of their origin, a taxonomist might understandably assign new specific or generic names to such new forms, which also undoubtedly occur in nature.

G. DECELIUS (Uppsala)

The Experimental Method in Lichen Taxonomy

Taxonomical investigations of lichens (lichenized fungi) are usually made according to a method that can be called the *directly observing and comparative method*. With this method, which is the primary one, we come a long way. In certain cases, however, it is insufficient, and then experiments—critically used—can be decisive. This *experimental method* must not be regarded as the opposite but as

a complement to the first-mentioned method, which is always a presumption of the latter.

The experiments—simple or more complicated—can be undertaken in the field as well as in the laboratory, dependent on the circumstances. The very slow growth of the lichens is to some degree an obstacle.

The experimental method can be used for illuminating either isolated cases of a special nature (separation of certain closely related types, etc.) or more general problems. I have since 1947 used this method in the taxonomy of *Collema*, viz. for studying the rôle of the fungal symbiont for the habitus of the different *Collema*-lichens (the consortia), in this connection of great importance. The main rôle for the habitus is here usually ascribed to the algal symbiont (*Nostoc*). I have in culture (on silicic gel and agar as well as on somewhat limy clay and in Bristol's solution) *Nostocs* isolated from about 10 species of *Collemataceae*, mainly *Collematata* (also free *Nostocs*). Though these *Collematata* are very dissimilar in habitus, their *Nostocs* are in the main rather similar (in some cases small but distinct differences occur with respect to the shape of the colonies, their rate of growth, etc.). The colonies develop best on the solid substrata, gel and agar (those on clay are still quite young), and are \pm globose or plate-formed (dependent on different moisture conditions), in the latter case up to some cm in diam. (when dry, they are smaller and more membrane-like). As in related free *Nostocs*, regular lobation is entirely absent. On gel and agar as well as in the solution the colonies produce diaspores, which can be called hormocysts (short or long chains of cells with a gelatinous sheath), very abundantly; more rarely hormogonia. The experiments seem to prove that the habitus of the different *Collema*-lichens is determined in almost the same degree by both symbionts—general shape, consistency, and colour by the alga, details concerning shape, size, lobation, etc., by the fungus. The consequence will be that these latter characters (from the fungus) are of the same diagnostical value in the species taxonomy as characters

from the spores, excipulum, etc. (I postulate that the taxonomy of the lichens means that of the fungal component only.) My experiments are not yet finished. Also synthesis experiments have been started.

P. W. RICHARDS (Bangor)

Taxonomy of Musci with Special Reference to Experimental Methods

Musci are unusually plastic organisms, and there is good reason for believing that the phenotypic variation of one genotype is commonly much more striking than the differences between nearly related genotypes when grown under identical conditions. Though this would indicate the necessity of experimental methods for a satisfactory taxonomy of mosses, they have been very little used. The taxonomy of 'difficult' groups, e.g. *Drepanocladus*, cannot be resolved without recourse to experiment.

In Musci as in other groups there are: a) 'Taxonomic' species and b) 'Natural' species. a) In Musci are defined almost entirely by morphological-anatomical characters, the phenotypic variability of which is not known. b) are 'genetically distinctive, reproductively isolated natural populations' (EMERSON). In the floristically better-known regions it should be the aim of bryophyte taxonomy to make the 'taxonomic' species coincide as far as possible with the 'natural' species by, i) utilizing characters of cell-organization, physiology, and ecology as well as the conventional morphological-anatomical characters; ii) investigating where possible the nature of the genetical or other barriers separating the natural populations. Both i) and ii) demand experimental methods. Work on such lines will no doubt demonstrate that 'taxonomic' species in Musci may be (in TURESSON's terminology) coenospecies, ecospecies, ecotypes, or ecads (modifications, sensu ВУСН). In addition to experimental work there is still scope for careful field observation, since there may be important ecological differences be-

tween populations showing only trivial morphological differences.

These general remarks were illustrated by references to *Tortula ruralis* and *T. ruraliformis*, the European *Orthodontium*, and to experimental work in progress on *Hypnum cupressiforme* and its varieties.

Discussion

W. MELJER: That several species of *Orthodontium* are probably widely spread over the world is demonstrated also by the fact that *O. gracilis* WILSON certainly also occurs in California, not only in Western Europe. See A. L. ANDREW in GROUT's Mossflora. Samples of this species collected in California are also identified by me in connection with work on this genus. By analogy it is more probable that *O. lineae* occurs as well in S. Africa as in Europe.

H. BUCH (Helsingfors)

Experimentelle Methoden in der Lebermoossystematik

Wenn der Hepatikologe im Freien ein Lebermoos findet, von welchem er nicht weiss, ob es eine Modifikation einer gewissen Art oder eine erblich verschiedene Form ist, kann er durch Kultur der beiden Formen unter genau den gleichen Aussenbedingungen eine sichere Antwort auf die Frage erhalten: Wenn sie Verschiedenheiten aufweisen, sind sie erblich verschieden. Bestehen doch die erblichen Unterschiede gerade in verschiedenen Reaktionsweisen auf ein und denselben Aussenfaktor! Wenn die derart zusammen aufgewachsenen Formen miteinander übereinstimmen, so müssen wir sie noch unter einigen anderen Konstellationen der Aussenbedingungen zusammen wachsen lassen, um etwas entscheiden zu können. Es könnte nämlich sein, dass sie auf einige in der ersten Konstellation nicht vorhandene Aussenfaktoren verschieden reagieren würden. Wenn sie auch in den späteren Konstellationen der Aussenbedingungen in morphologischer Hinsicht und durch ihre Färbung in

gleicher Weise reagieren, so sind sie in systematischer Hinsicht identisch (Beispiele solcher Kulturen u. a. bei BUCH 1922 und 1936). Genotypisch identisch brauchen sie deshalb nicht zu sein; gibt es doch auch solche genotypische, z. B. physiologische Unterschiede, welche dem Systematiker verborgen bleiben.

Die soeben beschriebene experimentelle Methode ist namentlich von Bedeutung, wenn die zu vergleichenden Formen nie oder selten in der Natur zusammen vorkommen. Bei Arten, welche gleichartige Standorte bewohnen, kann dieses Experiment schon in der Natur verwirklicht sein, z. B. bei *Riccia*.

Experimente, welche darauf hinzielen, die Reaktionen der Lebermoose auf die verschiedenen Aussenfaktoren kennenzulernen, sind ebenfalls für den Hepatikologen wichtig. Hier einige Beispiele solcher Reaktionen:

Die Braun-, Rot- oder Violettfärbung der Zellwände bei zahlreichen Lebermoosen ist, wie ich durch Versuche festgestellt habe, eine Reaktion auf direktes Sonnenlicht. Solche gefärbte Modifikationen sind als erblich verschiedene Formen behandelt worden. Das bekannteste Beispiel bilden *Scapania dentata*, *Sc. undulata* und *Sc. ambigua*, welche sich alle drei in meinen Kulturen als Modifikationen einer *Sc. undulata* zu benennenden Art erwiesen haben.

In feuchter Luft verlängern sich die Internodien bei vielen Lebermoosen, bei einigen sogar ansehnlich, in trockener Luft bleiben sie aber kurz, ganz unabhängig von der Lichtstärke. Dicht beblätterte Modifikationen sind bisweilen als besondere Arten beschrieben worden. Ich habe z. B. feststellen können (BUCH 1933), dass die in Helsingfors (Finnland) aufbewahrte Exsikkat-Probe der *Lophozia confertifolia* SCHIFFNER solch eine Modifikation von *L. Wenzelii* ist, mit der sie in Blattform und Zellnetz übereinstimmt. *Sphenolobus rigidus* (LINDBERG) K. MÜLLER ist eine dichtbeblätterte Pflanze, welche *Sph. minutus* habituell etwas ähnelt. Ihre Blattform und ihr Zellnetz ist jedoch fast das gleiche wie bei *Gymnocolea inflata* (vorher nicht veröffentlichte Mitteilung), obgleich die Pflanze habituell von der gewöhnlich

lockerblättrigen *G. inflata* der Wassertümpel sehr verschieden ist. Hängt doch der Habitus von der Internodienlänge wesentlich ab!

Bei den meisten solcher Lebermoose, deren Internodien auf den Feuchtigkeitsgrad der Luft reagieren, sind auch die sekundären Wandverdickungen der Blattzellen von diesem Aussenfaktor abhängig: sie entstehen überhaupt nur in Luft mit Feuchtigkeitsdefizit und werden um so stärker, je stärker dieses ist. Da die sekundären Zellwandverdickungen meistens gute systematische Merkmale abgeben, müssen wir feucht gewachsene, mit dünnen Zellwänden ausgestattete Lebermoose in trockener Luft kultivieren, um solche zu erhalten. Die mit mächtigen Zellwandverdickungen versehenen Modifikationen einiger Arten sind als besondere Arten beschrieben worden. Z. B. *Lophozia guttulata* (LINDB.), *Scapania Jörgensenii* SCHIFFNER (vgl. BUCH 1933, 1928) und *Sphenolobus saccatulus* (LINDB.) K. M. (vorher nicht veröffentlichte Mitteilung) sind solche Modifikationen von *L. porphyroleuca*, bzw. *Sc. nemorosa* und *Sph. minutus*.

Durch das experimentelle Studium der Lebermoosreaktionen auf die verschiedenen Aussenfaktoren bekommen wir selbstverständlich ein bedeutend reichlicheres Material zu den Artbeschreibungen als durch die blosse Beobachtung in der Natur und werden die Arten leichter zu wiedererkennen, auch wenn sie in der Natur in mehreren Modifikationen auftreten. Es müssten also so viele Arten wie möglich auf ihre Reaktionen hin untersucht werden.

Wie schon aus den wenigen hier erwähnten Beispielen hervorgeht, gibt es ausser den artspeziellen auch allgemeine, für zahlreiche Arten gemeinsame Reaktionen auf die Aussenfaktoren, welche für den Hepatikologen gleich wichtig sind. Sie sind noch wenig bekannt. Einige von ihnen sind von der Art der Wasser- und Mineralstoffversorgung unabhängig (z. B. die Dunkelfärbung der Zellwände in direktem Sonnenlicht und das Kleinbleiben der Blätter und Thallusflügel in schwachem Licht), andere hängen aber deutlich mit dieser zusammen. Z. B. das vorhin erwähnte Verhalten der Inter-

nodien und Zellwandverdickungen bei verschiedenen Luftfeuchtigkeitsgraden ist für die s. g. mixohydrinen Lebermoose (BUCH 1947, S. 23–25) charakteristisch, welche Wasser nebst Mineralstoffen bei trockenem Wetter mit Hilfe von Rhizoiden aus der feuchten, lockeren Unterlage aufnehmen und, wie die Gefässpflanzen, innen zu den Wasser verdunstenden Teilen leiten, in nassem Zustande aber mit allen ihren Aussenwänden aufnehmen, welche dann ungewöhnlich durchlässig sind (Plasmolyse mit Rohrzucker!).—Ganz andere Reaktionen auf die Aussenfaktoren werden die in dieser Hinsicht noch nicht untersuchten Pollakauofyten (BUCH 1947, S. 29, 30) zeigen (z. B. *Ptilidiaceae*, *Lejeuneaceae*, *Radulaceae* und *Frullaniaceae*). Sie bewohnen solche Unterlagen, welche nach dem Aufhören der Wasserzufuhr sofort eintrocknen (z. B. nackte Felsen und Baumrinde) und trocknen dabei auch selbst ein. Sie können sich also nur in nassem Zustande ernähren und entwickeln. Trotzdem sind ihre Internodien oft sehr kurz (z. B. *Herberta* und *Temnoma*) und ihre Zellwandverdickungen oft ansehnlich (z. B. *Herberta* und *Ptilidium*).—Die für die endohydrinen (BUCH 1945, S. 12) Lebermoose (haupts. *Marchantiaceen*) gemeinsamen Reaktionen sind ebenfalls unbekannt, obgleich *Marchantia polymorpha* zu den experimentell am eingehendsten untersuchten Moosen gehört, weil noch zu wenig Arten untersucht worden sind.

Litteratur

- BUCH, H.: 1922 in Societas Scientiarum Fennica, Commentationes Biologicae I, 4.
— 1928, ibid. III, 1.
— 1933, in Annales Bryologici VI.
— 1936, in Memoranda Societatis pro Fauna et Flora Fennica 11. 1934–1935.
— 1945, in Soc. Scient. Fenn., Comm. Biol. IX, 16.
— 1947, ibid. IX, 20.

Discussion

W. MELZER: Die Gefahr bei der Entdeckung von genetischen Unterschieden zwischen Lebermoosformen ist heute, dass man die Formen zu viel als einzelne Arten beschreibt und aufrecht erhält. Die experimentelle Methode bei höhe-

ren Pflanzen hat gezeigt, dass innerhalb einer natürlichen Art (vgl. Dr. RICHARDS Vortrag) sehr oft verschiedene erbliche Formen vorkommen. Was ist Dr. BUCHS Ansicht darüber? Wie soll man hier arbeiten?

IRENE MANTON (Leeds)

Experimental Methods Available for the Taxonomy of the Pteridophyta

Most of the cytogenetic methods available for the taxonomy of Flowering Plants can be used in the Pteridophyta although certain modifications are necessary to deal with the very high chromosome numbers and slow growth. In addition, owing to the separate gametophyte, a few special methods can be used. The principal technical details will be found in the appendix to "Problems of Cytology and Evolution in the Pteridophyta" (MANTON, 1950) which is not out but a proof copy is demonstrated. The principal methods are:

1. Comparative culture to show range of plasticity or constancy of characters.

2. Investigation of reproductive mechanism to distinguish between apogamous, sexual, or sterile forms, the latter being almost invariably hybrids.

3. Chromosome counts. These are important in detecting: a) hybrids where uneven somatic numbers are found, e.g. in triploids; b) cases where several genetically different forms have been compounded under one specific name. Many examples of both are in the European flora.

4. Chromosome pairing in known or sus-

pected hybrids gives evidence confirming the suspicion of hybridity and also indicates the nature of the relationship between the hybridizing species. Many common species can be shown to be allopolyploids by this means.

5. Special experimental methods appropriate to Pteridophyta are: a) induced apogamy and b) induced apospory. The latter is the easiest method of obtaining autopolyploids for comparison with wild polyploids. The former is a means of detecting further cases of allopolyploidy by means of the pairing behaviour in the apogamously produced plants.

6. Comparative chromosome numbers among genera are important in indicating phyletic affinities on the one hand and parallel evolution of morphological characters on the other.

Illustrative examples of all these categories are given. The principal taxonomic conclusions to which they have led may be listed as: a) the deletion of several sterile hybrids from the status of taxonomic species; b) the detection of numerous cases in which new taxonomic species will be required to separate genetically and cytologically distinct elements which have previously been confused; c) recognition of the fact that some much used taxonomic characters, notably the shapes of the sori in *Dryopteris* sens. lat. and *Athyrium*, are liable to be polyphyletic in origin and less reliable for diagnostic purposes than has sometimes been thought. On the other hand some less used characters, such as the spore pattern in *Cystopteris* or the annulus characters in *Polypodium*, may be highly reliable when supported by the cytology.

SESSION 2

Jointly with Section MXC: July 14th, 9 a. m. — noon, See page 393

SESSION 3

Jointly with Section MXC: July 14th, 1—4 p. m., See page 400

SESSION 4

Jointly with Section MXC: July 17th, 9 a. m. — noon, See page 412

SESSION 5

July 17th, 1—5 p. m.

Chairman: H. DES ABBAYES, Recorder: J. A. NANNFELDT

SUBJECT:

Lichens

S. AHLNER (Uppsala) *Some Aspects of Nomenclature and Taxonomy of Lichens*

SCHWENDENER's theory of the composite nature of the lichen thallus has for a long time been accepted by the lichenologists. The nomenclatural and taxonomical consequences of that theory, however, have hitherto been drawn only to a minor extent. The subject of this paper is a discussion of some more or less formal problems in connection with the adaptation of the dual hypothesis as the basis of scientific lichenology.

Ever since the investigations by FAMINTZIN & BARANETSKY (1867), the algal elements of the lichen consortia have been referred to the corresponding genera of free-living algae. The fungal component remained to be named and classified. According to the ideas of SERNANDER (1907), FINK (1911, etc.), DU RIETZ (1926, 1945), NANNFELDT (1932), and most Swedish lichenologists of the present-day, the lichen fungus receives the name originally given to the consortium. From this point of view the creation of a separate nomenclature for the fungal components (à la "*Xanthoriomyces parietinae*") is entirely unnecessary. However, the application of lichen names must be precisely formulated in the rules of botanical nomenclature. In two proposals (nos. 4 and 7) to Art. 64 the interpretation urged has been proposed.

As a consequence of SCHWENDENER's theory, the lichenized fungi must be included in the mycological system and their taxonomy worked out on a purely mycological basis. The family concept hitherto used must be subject to radical alterations in connection with the exclusion

of algological elements from the diagnostic characters. The lichen families have often got a more restricted circumscription than the corresponding units in mycology. For instance, *Teloschistaceae* and *Caloplacaceae* are so closely related that they as well could be united. The *Lecanoraceae* and *Lecideaceae* (and parts of the *Patellariaceae*) may probably form a well-defined unit of the rank of family.

The limitation and nomenclature of genera must also be brought into accordance with the principles mentioned above. There is no meaning in separating genera only with reference to the presence or absence of algae (e.g. *Buellia* and *Karschia*) or to the occurrence of different types of algae (*Coniocybe* and *Chroocybe*). The nomenclatural problems deriving from the different starting points for lichens and for non-lichenized ascomycetes may be more easily solved with a common starting point for all generic names (1753).

R. SANTESSON (Uppsala)

The New Systematics of Lichenized Fungi

It is remarkable that in most plant systems lichens are still treated as a separate class, sometimes named a form class, comparable with Fungi Imperfecti. Not even practical reasons can be stated for the preservation of such a Lichen class. From a taxonomical point of view we have to deal with lichenized fungi, not with lichens. The concept of lichen is a biological one. "Lichen systematics" based on algal characters is as unnatural as, e.g., a system of *Uredinales* based on characters from the host plants.

The "subclasses" *Ascolichenes* and *Basidio-*

lichens must axiomatically be rejected. *Cora* is to be referred to *Thelephoraceae* and is probably to be included in some already existent fungus genus.

As stated by NANNFELDT (1932), lichenized ascomycetes are found in *Ascoloculares* as well as in *Ascohymeniales*. In ZAHLBRUCKNER's system members of these two groups have been united, e.g., in the families *Graphidaceae* and *Pyrenulaceae*. Most lichenized fungi, "*Pyrenolichenes*" as well as "*Discolichenes*", belong to *Ascohymeniales*, and are to be referred to the orders *Sphaeriales* and *Lecanorales*, respectively. (Even the latter comprises a number of non-lichenized fungi.) The following is a very preliminary scheme of the taxonomical position of the lichenized Ascomycetes:

Ascoloculares.

Pseudosphaeriales: *Pleosporaceae* (e.g. *Arthopyrenia*), *Opegraphaceae*, *Arthoniaceae*, *Roccellaceae*.

Ascohymeniales.

Sphaeriales: *Porinaceae*, *Pyrenulaceae* (emend., excl. *Porina*, *Arthopyrenia*, a. o.), etc.

Lecanorales: *Graphidaceae* (emend., excl. *Opegrapha* a. o.), *Thelotremales*, *Asterothyriaceae* (emend.), *Gyalectaceae*, *Lecideaceae*, *Teloschistaceae*, and others.

Caliciales? Probably forming a separate order, but must be studied more carefully.

Most of the lichen families, as hitherto delimited, should be revised, and a number of them are to be rejected. E.g., *Coenogoniaceae* is to be included in *Gyalectaceae*, and *Strigulaceae* in *Porinaceae*, as they are "gonidial families" only. *Pyrenulaceae* (emend.) is not characterized by its gonidia but mainly by its spore type (spore cells lentiform), like that of *Graphidaceae* and *Thelotremales*. "*Pyrenothamniaceae*" and *Dermatocarpaceae* should be included in *Verrucariaceae*, as they are distinguished by a better developed thallus only. *Byssolomataceae* is to be referred to *Lecideaceae*.

The delimitations of lichen genera are now very often unnatural. "Gonidial genera" such as *Phylloporina*, *Paraphysothele*, *Allarthonia*,

Arthoniopsis, *Fouragea*, *Lecaniopsis*, etc., must be rejected. Most genera of crustaceous lichens are very schematically based on the spore septation only. For practical reasons we have to accept some of them provisionally until they have been treated monographically, but we must always try to find the natural delimitation of the genera. E.g. *Micarea* (cp. HEDLUND 1892) seems to be a good autonomous genus. Certain species of *Bacidia* and of *Lopadium* have to be transferred to the genus *Tapellaria*. Species with spores only transversely septated as well as such with muriform spores must be included, e.g., in the genera *Trichothelium* and *Tricharia* Fée.

Discussion

H. DES ABBAYES: Pour la classification des Lichens basée sur la nature du Champignon, il sera nécessaire de tenir compte également de la structure de l'ascogone (travaux de MOREAU) et de la structure de l'appareil apical de l'asque (travaux de CHADEFAUD et élèves).

E. DAHL (Oslo)

On the Use of Lichen Chemistry in Lichen Systematics

Investigations in the contents of lichen substances in the northern species of *Cladonia*, *Parmelia*, and *Cetraria* give many examples that lichen chemistry may be helpful in distinguishing difficult lichen species, but instances are found where morphologically inseparable individuals contain different lichen substances (*Cladonia chlorophaea*, *Parmelia furfuracea*).

The investigations show that lichen chemistry may be helpful also in distinguishing higher units than species. Subdivisions of *Cladonia* are confirmed by lichen chemistry, and hints toward improvements of the system are found. The investigations in the Norwegian *Parmelia* species by Mrs. H. KROG (still unpublished) give beautiful examples of the usefulness of such investigations. Both chemical and anatomical characters indicate that *Parmelia* subg. *Hypo-*

gymnia, *Parmelia furfuracea*, and the *Cavernularia* species are closely related. Most of the more important subdivisions of *Parmelia* are confirmed, and decisive arguments may be found in many dubitable cases.

The members of the genus *Cetraria* fall into two different groups. One group (*Cetraria glauca*, *lacunosa*, *chrysantha*, and *collata*) resembles chemically *Parmelia* subg. *Amphigymnia*, and subsequent anatomical investigations have confirmed the relationship. It is proposed to revive the old genus *Platysma* in amended state for these species. The other *Cetraria* species differ both chemically and anatomically from *Platysma* and have probably arisen from some ancestor resembling the brown *Parmelia* species. The *Nephromopsis* species are more closely related to *Cetraria* than to *Platysma*.

In accordance with a proposal by I. MACKENZIE LAMB it is recommended that morphologically indistinguishable lichen individuals which contain distinct lichen acids should be regarded as belonging to one and the same species, and that their chemical differences should be expressed by the use of the term "Strain" (German "Stamm", French "Lignée", Spanish "Lijnaje"), termed after the characteristic compound or compounds (if necessary with a query if not identified with certainty by analytical tests), together with the specific or subspecific epithet (in quotation marks) by which the strain in question is represented or has been formerly designated provided such an epithet already exists.

Examples:

Stereocaulon Wrightii TUCKERM. Stictic acid or typical strain.

Lobaric acid or "apocalypticum" strain.

Stereocaulon tomentosum FR. Stictic acid or typical strain.

Lobaric acid or "Sasakii" strain.

Stereocaulon albicans TH. FR. emend. LAMB.

Psoromic acid? or typical strain.

Atroranic acid or "gracilescens" strain.

Stictic acid or "subgracilescens" strain.

Cladonia chlorophaea (FLK.) Acid free strain. Cryptochlorophaeic acid or "cryptochlorophaea" strain.

Merochlorophaeic acid or "merochlorophaea" strain.

Grayaninic acid or "Grayii" strain.

Novochlorophaeic acid strain.

Hypogymnia furfuracea (L.) KROG. Physodic acid or typical strain.

Olivetoric acid or "olivetorina" strain.

Discussion

H. DES ABBAYES: Il faut être très prudent dans la généralisation de cette méthode, car l'expérience prouve qu'il existe presque toujours des exceptions embarrassantes. Par exemple: *Cladonia coccifera* de Tristan d'Acunha qui contient de l'acide fumarprotocétrarique, inconnu par ailleurs dans l'espèce européenne et dans tout le groupe des *Cocciferae*.

V. J. GRUMMANN (Berlin-Steglitz)

The Uniformity of the Terminology of Mycology and Lichenology

In the last 150 years many satisfactory results have been produced in mycology and lichenology. But during all this time and still to-day the formulation of the scientific facts suffers from the nomenclature-disease as well as from another defect: the varied use of the scientific terminology in Latin diagnoses and in scientific works and essays of systematic or other contents, may they be written in German or other languages. This confusion of the terms prevailing to-day is—under historical aspects—comprehensible for different reasons and therefore it may be justified. Some special examples may explain this: the same technical term is used by the different authors in an often very diversified sense; so each author is forced to explain his own terminology. Even in one work the terminology is varying. All attempts of some authors to settle the terminology were not generally accepted, for they were insufficient and had not enough emphasis to be generally recognized.

The subject of this discourse was started by Swedish colleagues in 1948. They suggested to make proposals to this Congress to uniform the terminology.

During his preparatory studies the author acknowledged more and more that such a proposal cannot be made by one lichenologist for he has to include the range of mycology, too. It is but the Congress that can give a stimulation promising success: it has to resolve the formation of a commission for both disciplines, fungi and lichens. This commission is ordered by the Congress to submit definitive proposals at a fixed time.

By this the speaker invites to form this commission and asks the members of the Section Taxonomy: Cryptogams to give their opinion in regard to a proposal he would be glad to find accepted:

1. The final uniformity of the terminology in mycology and lichenology is necessary and cannot be put off any longer.

2. The *termini technici* are to be fixed by a commission.

3. The members of this commission are to be proposed and to be chosen, if possible, before the end of this Congress.

4. Before being dissolved the Congress has to fix the time when the definite proposals have to be submitted.

5. The names of the members of this commission and the special branches of the co-workers are to be published in a proper place to enable all those colleagues interested in this subject but not present to-day to stimulate the members of this commission in their reform of the terminology.

A. H. MAGNUSSON (Göteborg)

On Descriptions of Lichens

Historical aspects. Soon after the introduction of the binominal nomenclature we find rather long descriptions in Latin, often combined with more or less good illustrations. With the creation of numerous genera, e.g. 23 in ACHARIUS, Methodus Lich. 1803, the descriptions

could be limited to the decisive characteristics of closely related species, and they were improved by ACHARIUS in his Lich. Univ. 1810.

The introduction of the microscope had at first the result that less stress was laid on morphology and that spore characters and data on the apothecial structure were included in the descriptions. In TH. FRIES, Lich. Scand., we find a type of descriptions that has hardly been surpassed in clearness, in balanced and precise wording, and in typographic arrangement. Too short descriptions, e.g. those of NYLANDER and RÄSÄNEN, are not sufficient now that the species conception has become rather narrow, and many structural details must be considered that were not necessary formerly. But on the other hand, VAINIO's, HUE's, ZAHLBRUCKNER's and especially LETTAU's long, typographically too uniform descriptions render it difficult to grasp the decisive characteristics of the species in question.

Different kinds of descriptions. A. Of new species.—A new species must now be described in Latin to be valid, and we have to choose between a full description entirely in Latin or a short one with the essential characteristics in Latin completed by further details in another language. If the first form is used, the main characteristics ought to be emphasized in print by using italics or spaced-out letters, or they ought to be discussed separately afterwards. Since we do not know whether structural details now considered unimportant may, perhaps, be of greater value in the future, as many details as possible ought to be recorded and also the effect of reagents now used, even if the author does not believe in their value in taxonomy. A uniform method of describing the different lichen parts is also desirable.

B. In a flora.—The descriptions here must be shortened to a certain degree, dependent on its purpose—very short in a flora for beginners but more detailed in a more scientific one. In the latter case, a rapid conception of the main characteristics is facilitated by the means mentioned above and the uniform arrangement of the characteristics. The habitat

should be given in detail if possible, and the distribution of the species in general outlines. As a complement to the descriptions an elaborate key must be given, not necessarily consistently dichotomous but with several characteristics in the line ending with the species name.

H. DES ABBAYES (Rennes)

Les Cladonia du sous-genre Cladina: *essai de classification naturelle*

Dans notre Monographie des *Cladina* (1939), nous avons rangé les 11 espèces alors connues dans 3 sections: *Impezae*, *Tenuis*, *Rangiferinae*. Depuis cette date, le nombre des espèces décrites est passé à 22 et les affinités des espèces entre elles se trouvent mieux dégagées, si bien qu'il est devenu nécessaire, ainsi que nous le laissons prévoir (1947), de remanier certaines sections et d'en créer de nouvelles. Notre classification reste avant tout basée sur le type de ramification des podétions et sur l'aspect des extrémités, caractères qui déterminent les affinités naturelles. La présence d'une matière rouge ou incolore dans les conidanges est un caractère paraissant, pour l'instant du moins, constant dans toutes les sections, sauf une. Mais cette seule exception à la règle laisse prévoir qu'il ne peut être considéré comme un critère taxonomique déterminant. Quant aux caractères tirés de la couleur des podétions (jaune avec acide usninique, cendré sans acide usninique) et du goût (amer avec acide fumarprotocétrarique, doux sans acide fumarprotocétrarique), ainsi que les autres caractères chimiques, ils n'ont aucune valeur taxonomique générale, simplement une valeur spécifique (parfois même celle d'une variation individuelle).

Voici la classification que nous proposons, basée sur ces principes.

Sectio I: Bicornutae DES ABB. nova. — Podetia dichotomiis aequalibus vel subaequalibus ramosa, apicibus rectiusculis plus minusve divaricatis praedita. Conidangia materiam albidam continentia.

Cl. Evansi DES ABB. (1939) (albido-cinereus).

Cl. pseudoevansi ASAH. (1940), Cl. Skottsbergii H. MAGN. (1941), Cl. mediterranea DUVIGN. & DES ABB. (1947) (stramineo-flavescentes).

Toutes les espèces actuellement connues sont dépourvues d'acide fumarprotocétrarique.

Sectio II: Tenuis DES ABB. 1939, emend. 1950. — Podetia gracilia, praecipue dichotomiis inaequalibus ramosa, apicibus typice eodem latere deflexis, rectiusculis et plus minusve divaricatis praedita. Conidangia materiam coccineam continentia.

Cl. Sandstedei DES ABB. (1938) (albido-cinereus).

Cl. leiodea H. MAGN. (1941), Cl. subtenuis DES ABB. (1939), Cl. tenuis HARM. emend. DES ABB. (stramineo-flavescentes).

Cl. leucophaea DES ABB. (1936) (albido-cinereus).

Toutes les espèces connues contiennent de l'acide fumarprotocétrarique. Les trois premières espèces, par leurs extrémités subégales, et le plus souvent divariquées comme dans la section I, sont des termes de passage entre les deux sections. Le caractère de la courbure des extrémités d'un même côté constitue une tendance chez les espèces de la section, mais non un caractère constant.

Sectio III: Impezae DES ABB. 1939, emend. 1950. — Podetia polychotomiis, praecipue trichotomiis, in summo subaequalibus ramosa, apicibus attenuatis, rectiusculis et divaricatis, aut undique deflexis praedita. Conidangia materiam albidam continentia.

Cl. impeza HARM., Cl. confusa R. SANT. (1942), Cl. leptoclada DES ABB. (1947), Cl. fallax DES ABB. (1939) (stramineo-flavescentes).

Cl. polia R. SANT. (1942) (albido-cinereus). Seul Cl. fallax contient de l'acide fumarprotocétrarique.

Sectio IV: Alpestris DES ABB. nova. — Podetia polychotomiis, praecipue tetrachotomiis, in summo subaequalibus ramosa, apicibus crassis plus minusve obtusis, radiato-divaricatis praedita. Conidangia materiam coccineam aut albidam continentia.

Cl. alpestris (L.) RABENH., Cl. alpestroides DES ABB. (1947) (stramineo-flavescentes).

Les deux espèces sont dépourvues d'acide fumarprotocétrarique. La première possède une matière rouge dans les conidanges, la seconde une matière blanche.

Section V: Rangiferinae DES AB. 1939. — *Podetia robusta* praecipue polychotomiis typice inaequalibus ramosa, apicibus typice eodem latere deflexis praedita. Conidangia materiam albidam continentia.

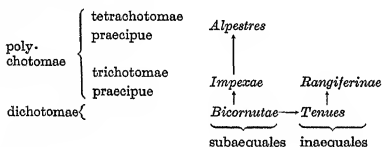
Cl. rangiferina (L.) WEB., *Cl. vicaria* R. SANT. (1942) (albido-cinerascentes).

Cl. sylvatica (L.) HARM. emend. SANDST., *Cl. mitis* SANDST. emend. EVANS, *Cl. laevigata* (WAIN.) GYELNIK, *Cl. submitis* EVANS (1943) (stramineo-flavescentes).

Les trois premiers contiennent de l'acide fumarprotocétrarique.

Note. — *Cl. signata* WAIN., incorporé dans le s. g. *Cladina* par SANTESSON (1942), ne peut y être maintenu, ainsi, que nous l'avons montré (DES AB., 1943), à cause de la présence de folioles sur les podétions. *Cl. subimpeza* DUVIGN. (1939) n'est qu'une variation accidentelle de *Cl. impeza* HARM. dépourvue d'acide usninique.

On peut résumer dans le tableau suivant les affinités phylogénétiques possibles de ces différentes sections:



H. RUNEMARK (Lund)

Taxonomy and Distribution of the Yellow Species of *Rhizocarpon* in Europe

In European material the following 10 species are recognized by the author:

Artificial key to the species

- 1 a. Spores 2-celled.
- 2 a. Thallus K—.
- 3 a. Medulla I + blue. Spores 12–18 × 6–9 μ.
- 4 a. Hypothallus absent.

1. *Rh. norvegicum* RÄS. [including *Rh. intermediellum* RÄS.], distributed in the Scandinavian mountains. Probably, it has in late time by geographical isolation been differentiated from the closely related *Rh. italicum*.—2. *Rh. italicum* RÄS., found in the Alps.—3. *Rh. superficiale* (SCHAER.) MALME [incl. *Rh. sphaericum* (SCHAER.) RÄS.], found in the Alps, one locality also in Spitzbergen.—4. *Rh. oreites* (VAIN.) A. ZAHLBR. [syn. *Rh. alpicola* (WG) RABH. pr. p.], a rather variable species found on most high mountains in Europe. Not in Arctic regions! Related species in Central Asia.—5. *Rh. simulans* H. MAGN. [incl. *Rh. occidentale* LYNCE and *Rh. crystalligenum* LYNCE], an arctic-atlantic species with outposts in the Pyrenees and the Alps. Certain types are indistinctly K + red.—6. *Rh. splendidum* MALME, found in one locality in Central Sweden only, but abundant there.—7. *Rh. chionophilum* TH. FR. [syn. *Rh. alpicola* (WG) RABH. pr. p.], a west-arctic species. Not in the Alps.—8. *Rh. chionophiloides* VAIN. Transitional types between this species and the closely related *Rh. chionophilum* are found (but rare) in Scandinavia. The species is very variable in Siberia, but rather uniform in Scandinavia.—9. *Rh. viridiatrum* (FLK.) KBR, widely distributed. In Europe its northern limit passes over Central Sweden and South Finland.—10. *Rh. geographicum* (L.) DC., an almost cosmopolitan collective species (in the Tropics only in high mountains) with many geographic races. It is polymorphous especially in high mountains, e.g. the Alps and the Scandinavian mountains. Types worth mentioning (most of them subspecies) are e.g. *lecanorinum* FLK., *diabasicum* RÄS., *pulverulentum* SCHAER., *conglomeratum* FR., and *feracissimum* MALME. The species is not yet sufficiently studied. RÄSÄNEN divided it uncritically in many species, varieties, and forms.

- 5 a. Thallus dispersed, very small (—5 mm). . . . *Rh. norvegicum* RÄS.
 5 b. Thallus continuous, not very small. *Rh. italicum* RÄS.
 4 b. Hypothallus present. Thallus continuous. . . . *Rh. superficiale* (SCHAER.) MALME
 3 b. Medulla I—.
 6 a. Spores 20–30 × 10–18 μ *Rh. oreites* (VAIN.) A. ZÄHLER.
 6 b. Spores 12–17 × 7–9 μ *Rh. simulans* H. MAGN.
 2 b. Thallus K + red.
 7 a. Spores 12–18 × 5–9 μ
 8 a. Medulla I + blue. *Rh. splendidum* MALME
 (8 b. Medulla I—. *Rh. simulans* H. MAGN.)
 7 b. Spores 24–30 × 11–15 μ
 9 a. Medulla I—. *Rh. chionophilum* TH. FR.
 9 b. Medulla I + blue. *Rh. chionophiloides* VAIN.
 1 b. Spores muriform. Thallus K—.
 10 a. Medulla I—. Spores with few septa. *Rh. viridiatrum* (FLK.) KBR.
 10 b. Medulla I + blue. *Rh. geographicum* (L.) DC.

O. ALMBORN (Lund)

Some Aspects of the Sociology of Epiphytic Lichen Communities

In lectures (from 1940 on) DU RIETZ proposed a division of the North European corticolous vegetation into "poor bark" and "rich bark" based upon a correlation between the acidity of the bark and the number of species in the corticolous communities (cf. Sv. Bot. Tidskr. 1945 p. 147). The poor bark with the federation *Physodion* is divided into "extreme poor bark" often with the union *Euphysodetum* (very poor in species) characteristic of the very acid *Pinus* and *Picea* bark (pH < 4), and "transitional poor bark" often with the union *Physodeto-sulcatetum* (somewhat more rich in species) characteristic of the not equally acid bark of *Quercus*, *Betula*, and *Alnus* (pH c. 4–5), in *Quercus* sometimes lower. The rich bark with the federation *Xanthorion* (rich in species) is met with in thin bark of chiefly *Populus tremula*, but also *Fraxinus*, *Acer*, and *Ulmus* (pH c. 5–7). Through the influence of dust, the poor bark of different kinds of trees can change into bearing rich bark vegetation (with *Xanthorion*), the pH values approaching 7.

In "Distribution and Ecology of some South Scandinavian Lichens" (Bot. Not. Suppl. 1: 2,

1948, p. 221), I expressed some criticism of this schematic classification. Further studies have confirmed the views propounded in my paper of 1948:

1. The correlation between pH values and number of species holds true only to a limited extent, chiefly in certain photophilous communities. There is no difficulty to find communities within *Physodion* containing as many or more species than communities within *Xanthorion*; and extreme facies of *Xanthorion* (e.g. on *Salix* at the roads of Skåne, S. Sweden) contain a very small number of species. Thus the terms "poor bark" and "rich bark", when based on the number of species in the communities, had better be avoided.

2. What names shall we choose instead? It is true that the federations *Physodion* and *Xanthorion* represent rather well-delimited aspects of the photophilous lichen vegetation: *Physodion* containing dust-free communities mainly on the trunks of forest trees, *Xanthorion* on dust-impregnated trunks of trees near roads. Through the admission that the dust-free bark of young *Populus tremula* has a vegetation resembling *Xanthorion*, we can characterize *Physodion* as coniofobous epiphytic vegetation, and *Xanthorion* as coniophilous. The term nitrophilous should be avoided, as it is

not proved that the species in question are favoured by nitrogen compounds exclusively. The influence of phosphoric compounds will certainly need an investigation.

3. The photophobic communities are mainly constituted by crustaceous lichens. They may be divided into *Graphidion* (on smooth bark; index species *Graphis scripta*) and *Leprarion* (on rough bark; index species *Lepraria aeruginosa*). As examples of the relations between these two federations on the one hand, and *Physodion* and *Xanthorion* on the other, the speaker demonstrated a summary of some analyses of lichen communities on *Fagus* and *Quercus* from the island of Hallands Väderö, NW. of Skåne.

Even after the addition of these two federations, there are several problems to be solved in epiphytic lichen sociology. The federation *Lobarion*, with species of *Lobaria*, *Nephroma*, etc. dominating, described by OCHSNER, plays a part in certain oceanic districts. The special communities on the bases of tree trunks and on small twigs have been studied only to a very limited extent.

Discussion

E. DAHL: I quite agree with Dr. ALMBORN that the number of species in the associations cannot be used as distinguishing character between *Physodion* and *Physcion*. In Nordmarken near Oslo societies belonging to *Physodion* with more than 20 species per analysis are found; that is more species than in the presented tables of *Xanthorion*.

The *Parmeliopsis-Cetraria pinastri* communities of the bases of trunks and tree-logs and on the small twigs of *Betula* evidently form a sociological entity by itself dependent on the bases of trees for snow-cover. The upper limit of the society seems to correspond to the *olivacea* line so well known from alpine regions.

J. J. BARKMAN: Some of the epiphytic lichen communities mentioned by the speaker have already been described by HILTZER (1925). Contrary to the study of OCHSNER (1928), which

is based on the Zürich-Montpellier method, the work of HILTZER, as well as that of ALMBORN, is based on the Uppsala method. It shows very well that also for epiphytic lichen communities the former method leads to the distinction of associations which are much more homogeneous in ecological respect than associations based on the latter method. This is especially well shown by those communities dominated by euryoecic species as *Parmelia physodes* or *Parmelia sulcata*. These species, according to their wide ecological amplitude, may be accompanied by species of widely different ecology.

As to the method used here it seems not justified to use always a quadrat of 8 square dm, because the size of the quadrat must depend on the minimum area, which is different for different communities: sometimes 8 sq. dm may be too large, sometimes too small. In the case of a large minimum area it may even be necessary to comprise corresponding parts of the surface of more than one tree into one quadrat survey.

F. MATTICK (Berlin-Dahlem)

Die Lichenologie in Deutschland seit 1870 und ihre Zukunftsaufgaben

Alles bis 1870 in der Flechtenforschung geleistet ist durch A. v. KREMPPELHUBER in seiner 3-bändigen „Geschichte und Literatur der Lichenologie“ (1867–72) zusammengestellt worden. Seitdem fehlt eine zusammenfassende Darstellung; sie ist durch den Berichterstatter als „Geschichte und Literatur der Lichenologie von 1870 bis 1950“ in Angriff genommen worden. — Seit 1870 sind von den Autoren in Deutschland, Österreich und den deutschsprachigen Gebieten der Schweiz gegen 1700 lichenologische Arbeiten veröffentlicht worden, das ist 1/3 aller in diesem Zeitraum überhaupt erschienenen lichenologischen Schriften.

Von den schon bei KREMPPELHUBER erwähnten älteren Lichenologen arbeiteten später noch (in Klammer Zeit der Tätigkeit, dahinter Zahl

der wichtigeren lich. Arbeiten): RABENHORST (-81) 5, KREMPELHUBER (-82) 15, KOERBER (-85) 10, LAHM (-88) 1, STIZENBERGER (-95) 25, MÜLLER-ARG. (-96) 150, ARNOLD (-01) 100, REHM (-18) 8.

Mit der Erkenntnis der Doppelnatur der Flechten durch SCHWENDENER begann eine neue Epoche der Lichenologie; an neuen Namen treten auf: KRABBE (82-96) 4, STEIN (72-99) 15, KERNSTOCK (76-00) 20, ZUKAL (78-00) 20, MINKS (73-01) 33, BRITZELMAYR (75-09) 30, ZOFF (92-09) 36, HESSE (80-16) 25, SENFT (95-22) 10, LINDAU (88-23) 31, STEINER (81-21) 43, FÜNFSTÜCK (84-25) 10, BITTER (98-28) 10, REINKE (94-32) 4, SCHULZ-KORTH (27-31) 7, NIENBURG (07-33) 5, ANDERS (99-36) 28, BACHMANN (86-27) 72, ZSCHACKE (08-37) 9, ZAHLBRUCKNER (85-38) 100, REDINGER (33-40) 17, HILLMANN (16-43) 31, ERICHSEN (07-45) 56, und von den noch jetzt Tätigen: SANDSTEDE (89-) 30, TOBLER (00-) 31, LETTAU (11-) 14, KEISSLER (09-) 20, SCHADE (12-) 10, FREY (23-) 20, GAMS (22-) 5, KLEMENT (31-) 10, MATTICK (29-) 25; GRUMMANN (31-) 6, SCHINDLER (35-) 14, LANGERFELDT (38-) 5; hinzu treten die zahl-

reichen Forscher, die nur eine oder wenige flechtenkundliche Arbeiten veröffentlicht haben.

Alle Arbeitsgebiete der Flechtenforschung wurden durch die Genannten weitgehend gefördert: Bibliographie, Phylogenie und Systematik, Floristik, Geographie und Soziologie, Morphologie und Anatomie, Vermehrung, Physiologie, Biologie, Methodik.

Wichtige Übersichtswerke gaben: FÜNFSTÜCK u. ZAHLBRUCKNER (in Natürl. Pfl.fam.) 1898 u. 1926, LINDAU u. SYDOW (Thesaurus) 1907-17, ZAHLBRUCKNER (Catalogus, 7360 S.) 1922-40.

Floren für das ganze Gebiet: KUMMER 1874 u. 83, SYDOW 1887, LINDAU 1913 u. 1923, ANDERS 1928, MIGULA 1929-31.

An der Neuauflage von RABENHORSTS Kryptogamenflora arbeiteten mit: ERICHSEN, FREY, HILLMANN, KEISSLER, REDINGER, SANDSTEDE, ZSCHACKE; sie fortzusetzen, ist eine der wichtigsten Zukunftsaufgaben.

Durch den Krieg wurden zahlreiche deutsche Flechtensammlungen vernichtet, darunter als die umfangreichsten die von BACHMANN, HILLMANN, KLEMENT, MINKS, SANDSTEDE, SCHADE und SCHULZ-KORTH.

SESSION 6

July 18th, 9 a. m. — 1 p. m.

Chairmen: W. R. TAYLOR and F. E. FRITSCH, Recorder: H. SKUJA

SUBJECT:

Algae: General Organization and Taxonomy, etc.

F. E. FRITSCH (Cambridge)

The Heterotrichous State

In a considerable proportion of filamentous algae or of those that commence their life as a filament, the primary development is effected by cell-division in various directions perpendicular to the substratum and results in a not uncommonly richly branched filamentous system that extends over the surface of the latter and is firmly attached to it. It is quite incorrect

to look upon this purely as a mechanism serving for anchorage, since at this stage it comprises the whole plant and consists of cells with well-developed chromatophores. It represents in fact the primary photosynthetic system of the plant, and it is only after the threads composing this system have gained a certain degree of vigour that division-walls parallel to the substratum also arise in some or many of the cells, leading to the formation of outgrowing filaments which it is convenient to speak of as the erect

system and which in later stages, usually after considerable ramification, may constitute the bulk of the plant. For those, who only examine the mature plants, the primary prostrate system may in such algae appear merely as a comparatively insignificant attaching mechanism, which is often indeed left behind upon the substratum, but actually it has played an important and indeed essential part in the development of the mature thallus. It is this dual development of the plant-body which I designate the heterotrichous state or heterotrichy, and I propose in a few words to point out its morphological, taxonomic, and evolutionary significance.

The simplest expression of this state, the heterotrichous filament, is found in all classes of algae that have evolved beyond the unicellular stages. It is well exemplified by many species of *Stigeoclonium*, *Trentepohlia*, *Ectocarpus*, *Sphacelaria*, *Erythrotrichia*, and *Acrochaetium*, *inter alia*, to mention only examples taken from the three main classes of algae. In all of these genera, however, the relative development of the two parts of the plant—the prostrate and erect systems—is subject to appreciable variation. In all, there are species (or perhaps sometimes merely environmental forms) in which the creeping prostrate system, then very perfectly developed, constitutes the bulk of the thallus and the offstanding branches are few, often unbranched and consist of only a small number of cells. By contrast there are other species (or forms) in which the creeping system is only a little-branched thread, completely overshadowed by the strongly developed and early arising erect system. Again in *Ectocarpus*, and possibly also in *Stigeoclonium*, there are species in which growth is erect from the first and in which the germinating spore straight away divides by walls parallel to the substratum. This condition is also found in many species of *Acrochaetium*. The plasticity of the heterotrichous state is one of its striking peculiarities.

There is an appreciable number of green and brown algae in which development scarcely passes beyond the prostrate stage before re-

production occurs. Such are many *Coleochaete*, *Aphanochaete*, *Pringsheimia*, *Streblonema*, and *Mikrosyphar*, while among Bangiales *Erythrocladia* exemplifies this type of plant. These algae show us one direction in which the heterotrichous filament has evolved. A far larger number of algae, however, have advanced in the other direction, with further development and often very marked elaboration of the erect system. This is so in comparatively few green algae, but there is reason to believe that most, if not all, Phaeophyceae have evolved from simple filamentous heterotrichous types, and among Rhodophyceae this mode of development is even more manifest.

The bulk of the isogamous brown algae, namely the *Ectocarpales* (in which I include the *Chordariales*, *Punctariales*, and *Dictyosiphonales* of KYLIN), the *Tilopteridales*, and the *Sphacelariaceae*, show very obvious heterotrichy in their early development. The first stages of these seaweeds consist of a system of richly branched threads spreading, often widely, over the substratum and not uncommonly so densely aggregated as to form an almost continuous discoid growth. The early stages of *Castagnea Zosteræ* as figured by SAUVAGEAU, of *Leathesia* or *Desmotrichum* as figured by KYLIN, of *Stictyosiphon* as depicted by ROSENVINGE, of *Aspercoccus* as shown by KUCKUCK, all illustrate this type of development, and many other instances could be cited. The erect threads arising from the prostrate growths develop in various ways, that are not our present concern, to give the mature thallus which may often be many centimetres in length. When this thallus has reached maturity, the original prostrate system, if it has survived, appears but as a diminutive structure at the base of the plant, but this may not mask the fact that it has served an all-important purpose during the early development. The early stages of these isogamous brown algae are all filamentous growths resembling an *Ectocarpus* or allied form, such as *Myrionema*.

The same is true of the haplobiontic Florideae, the *Nemalionales*, as well as of many of the *Cryptonemiales*, where the prostrate system,

from which the filaments giving rise to the mature uni- or multiaxial thallus arise, is usually a well-developed spreading growth, well shown by KILLIAN in *Dudresnaya*, by KUCKUCK in *Platoma*, by KYLIN in *Bonnemaisonia*, and so on.

While in the majority of heterotrichous algae, only some, and often only a few, of the cells of the prostrate system grow out into offstanding threads, there are in all classes genera in which all or at least a large majority of the prostrate cells give rise to short erect threads and produce crusts. Such crusts are seen for example in *Pseudopirngsheimia* among Chlorophyceae, in *Ralfsia* among Phaeophyceae, and in *Hildenbrandia* among Rhodophyceae. This habit is also exemplified in various Florideae where, while some of the erect threads progressively enlarge to form the mature thallus, the others form the basis of the often extensive and sometimes perennial attaching disc. Examples are furnished by *Dumontia* and *Polydides*.

In the heteromorphic brown algae that have attained to oogamy, the *Desmarestiales* and *Laminariales*, the early stages of the sporophytes are not heterotrichous, the germinating zygote producing an erect-growing filament from the first. The gametophytes, however, are still minute heterotrichous filaments and, apart from the other implications that these facts suggest, they justify the view that in the evolution of the sporophyte of these algae the prostrate system has been suppressed. Such a tendency is recognisable even among the species of *Ectocarpus*, as I have already pointed out.

The same conclusion is reached with respect to the two generations of the more specialised diplobiontic Florideae, if the early stages of their development are studied on a comparative basis. In various *Cryptonemiales*, and practically all *Gigartinales* and *Rhodymeniales* that have been investigated, the first few division-walls in the germings are still perpendicular to the substratum, but this only leads at the best to the production of a small mound of cells and not to a spreading expanse, before septa parallel to the substratum arise and the formation of

the erect system begins. In the *Ceramiales*, including the most highly specialised of the diplobiontic Florideae, we find the same early development as in *Desmarestiales* and *Laminariales*, the growth being erect from the first and the prostrate system being completely suppressed.

In this connection it is noteworthy that in *Draparnaldia* and *Draparnaldiopsis*, Green Algae which are vegetatively rather highly specialised as compared with their immediate allies, the prostrate system appears likewise to be suppressed. It seems, therefore, as though, with increasing specialisation in the heterotrichous Chlorophyceae, Phaeophyceae, and Rhodophyceae, elimination of the prostrate system has always occurred.

Heterotrichy affords a striking example of parallelism among the algae, but, whereas in the Chlorophyceae, in comparison to the class as a whole, it represents a high stage of development, in the two great marine classes it is most clearly shown among the less specialised members (*Ectocarpales*, *Nemalionales*), which probably in part afford us prototypes of what the ancestors of the more specialised members of these classes were like. This state of the plant-body appears to constitute an important evolutionary stage in the development of the thallus and to form the foundation upon which the more elaborate types of algal thalli have been built. Taxonomically it is important because it affords one of the characteristic features of the *Ectocarpales* among the brown and of the *Nemalionales* among the red algae.

There can be no doubt that the prostrate system of the heterotrichous alga represents a growth-form that is admirably suited to the colonisation of substrata in moving water. Heterotrichous types play a considerable rôle as lithophytes in rivers and their importance in a marine environment was very strongly impressed upon me when studying the growth on metal panels submerged in the sea in connection with observations on the fouling of ships. The prostrate system is excellently adapted for photosynthesis in shallow waters, while the

delay in the production of offstanding threads enables a broad surface of attachment to be established before the tensile strains, which act on the erect growths, come into play. It is not impossible that the creeping filamentous type may have been the first kind of multicellular plant-growth to arise in the littoral zone and that all others were secondary to it.

The heterotrichous plant commonly remains arrested in its early filamentous stages, which frequently produce reproductive organs with whose help such stages can be repeatedly propagated. This arrest is permanent on the part of the filamentous gametophytes of the heteromorphic brown algae, but it may also be displayed by the early stages of the sporophytes and, especially among Phaeophyceae, these plethysmothalli of SAUVAGEAU play an important rôle in enabling many seaweeds, represented by the macroscopic plant only at certain times of the year, to perpetuate themselves during the remaining period. Evidence is accumulating that similar heterotrichous filamentous stages also play a part in the survival of diverse Florideae. It is the firm attachment provided by the prostrate system that specially suits such stages to serve as a means of perpetuation during a part of the year when rough seas are frequent.

J. FELDMANN (Paris)

Les types d'alternance de générations chez les Algues et leurs relations avec la phylogénie et la classification

Contrairement aux Archégoniates, l'alternance cytologique de phases est parfois, chez les Algues, indépendante de l'alternance morphologique de générations.

Le cycle haplophasique, comportant la méiose à la germination du zygote, est généralement considéré comme primitif car beaucoup d'algues haplophasiques ont des caractères peu évolués. Chez ces Algues, une seule méiose compensant la gamie ne permet pas la réalisation de toutes les combinaisons chromosomiques possibles, ce

qui retarde l'évolution et explique la persistance chez les Chlorophycées haplophasiques de beaucoup de caractères primitifs à côté de caractères évolués (zygotes enkystés, oogamie, etc.).

Au lieu de considérer le cycle haplophasique comme primitif, parce qu'il est celui de groupes peu évolués, il faut admettre, que de tels groupes sont peu évolués parce que la possession d'un cycle haplophasique a retardé leur évolution. C'est le cycle haplodiplophasique, avec méiose au milieu du cycle qui paraît le plus primitif.

Ce cycle cytologique s'accompagne d'une alternance isomorphique entre gamétophyte et sporophyte susceptibles, en outre, de se reproduire semblables à eux-mêmes par spores directes.

L'évolution, s'accompagnant généralement d'un déplacement de la méiose, entraînera la réduction ou la suppression de l'une des générations.

Les Rhodophycées diplobiontes, possédant deux phases cytologiques et trois générations morphologiques (gamétophyte, carposporophyte, tétrasporophyte) ont un cycle particulièrement complexe dont l'origine pourrait être la suivante:

Les Rhodophycées primitives auraient présenté une alternance isomorphique entre gamétophyte et sporophyte susceptibles de se reproduire par spores directes, le zygote étant libéré après la fécondation, comme cela a peut-être encore lieu chez certaines Protofloridées.

Ultérieurement, le zygote se développant en parasite sur le gamétophyte donnerait un carposporophyte à appareil végétatif réduit et portant indistinctement des spores directes produisant un sporophyte indépendant et des méiotospores reproduisant le gamétophyte. Une spécialisation ultérieure du carposporophyte ne produisant plus que des spores directes d'où naîtrait un sporophyte ne produisant que des méiotospores, réaliserait le cycle des Rhodophycées diplobiontes actuelles.

Une spécialisation inverse du carposporophyte ne produisant que des méiotospores, réaliserait un cas comparable à celui du *Liagora tetrasporifera*; tandis qu'un déplacement de la

méiose à la germination du zygote, frappant certaines formes d'un ralentissement dans leur évolution, aboutit au cas actuel des Némaliolaires haplobiontes.

De telles modifications du cycle, ayant eu lieu à divers moments de l'évolution, s'observent dans les divers ordres de Rhodophycées. Les différents types d'alternance de générations, bien que constituant un caractère phylogénétique important, ne peuvent donc servir de base pour la distinction des grandes subdivisions des différentes classes d'Algues, car l'évolution de ce caractère ne coïncide pas toujours avec celle des caractères morphologiques sur lesquels repose la classification.

Discussion

M. CHADEFAUD: 1. Les Phéophycées primitives et certaines Rhodophycées suggèrent que les Algues ont eu primitivement un cycle indéfini, dans lequel chaque individu pouvait produire, au gré des circonstances: des spores équationnelles, des gamètes équationnels, des spores réductionnelles et des gamètes réductionnels. Les gamètes équationnels conduisaient de N à $2N$, puis $4N$, $8N$ etc., chromosomes, tandis que les spores réductionnelles produisaient l'évolution inverse. Les cycles actuels dérivent du cycle indéfini ainsi réalisé par réduction aux phases à N et $2N$ chromosomes, et spécialisation en divers sens.

2. Pour expliquer que les *Chlorophycées oogames* sont toujours des haplobiontes haploïdes, on peut supposer l'évolution suivante:

a) ancestralement, le contenu des oogones se subdivisait en plusieurs gamètes femelles, qui étaient ensuite fécondés, d'où des zygotes générateurs de sporophytes $2N$; le cycle était diplobiontique:

b) aujourd'hui, ce contenu est d'abord fécondé (oosphère fécondée); sa division n'intervient qu'ensuite. Cette inversion fait que la division est une méiose, qui compense immédiatement la gamie. Le cycle est ainsi devenu haplobiontique haploïde.

P. DANGEARD: Je ne crois pas que la méiose

soit le phénomène fondamental ou pour mieux dire essentiel car la méiose est un phénomène dérivé, secondaire, qui a suivi la gamie comme une conséquence.

Dans l'évolution on doit admettre, non l'apparition de la méiose à un moment donné, comme le veut DARLINGTON, par modification d'une mitose ordinaire, mais l'introduction, dans le cycle évolutif, de la gamie et de la caryogamie avec la méiose comme conséquence.

Quel est le cycle évolutif le plus primitif? D'après M. FELDMANN cela pourrait être un cycle de diplobionte ayant une alternance entre deux phases égales. Il invoque le fait que dans un tel cycle la méiose produit le maximum de diversification. Or le même résultat peut être obtenu par la multiplication de nombre des œufs chez un haplobionte comme le *Chlamydomonas*.

Pour ces raisons nous considérerons plutôt que le type d'algue haplobionte, mode *Chlamydomonas*, est primitif.

B. J. LUYET: On peut concevoir un cycle biologique très simple (le cycle est mentionné dans mon travail « Comparative Study of the life Cycles of Lower Protozoa and Protophyta », *Biodynamica*, Vol. 6, 1950) — peut-être primitif — dans lequel un zygote se divise méiotiquement et forme immédiatement des gamètes. Dans ce cas la méiose est à la fois zygotique et gamétique; le seul élément diploïde est le zygote et les seuls éléments haploïdes sont les gamètes. Si on suppose qu'une série de divisions végétatives du zygote est insérée dans ce cycle avant la méiose, on obtient un cycle typique de diplonte, avec méiose gamétique; si les divisions végétatives sont insérées après la méiose, on a un cycle typique de haplonte avec méiose zygotique.

M. CHADEFAUD (Paris)

Les cellules flagellées des Algues et leur importance systématique

Tant chez les *Procaryotes* (*Cyanophycées*, puis *Bactéries*) que chez les *Eucaryotes* (*Rhodophy-*

cées, puis *Chromophycées*, sans amidon intraplastidial, et *Chlorophycées*, à amidon intraplastidial) les embranchements les plus archaïques (*Cyano-* et *Rhodophycées*) ont des pigments tétrapyrrol-protéiques, et pas de cellules nageuses; chez les autres, il y a eu suppression des tétrapyrrolprotéides, et apparition de cellules flagellées.

Du côté des *Eucaryotes*, seuls envisagés ici, tant chez les *Chromophycées* (*Pocillophyceinées* = g. *Pocillomonas*) que chez les *Chlorophycées* (*Prasinophycinées* = g. *Pyramidomonas*, *Platymonas*, *Prasinocladus*, etc.), ces cellules ont été primitivement pourvues d'une symétrie axiale avec, au pôle antérieur, un cratère vestibulaire, au fond duquel sont insérés les fouets, tous semblables entre eux.

Chez les *Chromophycées*, ce cratère s'est d'abord égueulé en une fente vestibulaire longitudinale ventrale, tandis que le nombre des fouets se réduisait à deux, qui devenaient dissimilaires, l'antérieur souvent onduleux et pleuronématé. Cela a donné:

1. *Cryptophycinées*: fente ventrale compliquée par une invagination postflagellaire garnie de trichocystes;

2. *Phéophycinées*: fente transformée en une fossette large et peu profonde par suppression de son flanc droit;

3. *Dinophycinées*: idem, mais fossette ensuite réduite à un système de trois sillons: présulcus, sulcus pour le fouet postérieur, et cingulum pour le fouet antérieur, avec puits flagellaires pour l'insertion des fouets, et pusules excrétrices débouchant dans ces puits;

4. *Raphidophycinées* (*Chloromonadines*): id., mais suppression du présulcus;

5. *Euglenophycinées*: suppression au contraire du cingulum; photocepteur sur la base d'au moins un des fouets chez les types chlorophylliens;

6. *Chryso-* et *Xanthophycinées*: appareil vestibulaire sans doute voisin de celui des *Dino-* et *Euglenophycinées*, car on retrouve pusule et photocepteur, mais il est atrophié.

Chez les *Chlorophycées*, l'égueulement en une fente ventrale est au contraire exceptionnel

(g. *Trichloris*). L'évolution s'est faite dans un sens très différent, que suggère l'étude des *Prasinocladus* et *Chlorodendron*, et qui conduit des *Prasinophycinées* aux *Euchlorophycinées*: rapprochement des bords du cratère, le convertissant en une chambre à orifice étroit; suppression de cette chambre par soulèvement de son plancher, venant s'unir au plafond; formation d'une papille flagellaire constituée par le centre du plancher, saillant dans l'orifice de la chambre. Cette évolution a laissé les fouets généralement semblables entre eux (isokontes), rarement pleuronématés (*Haematococcus*), ordinairement acronématés.

L'évolution des cellules flagellées s'accorde ainsi avec une classification rationnelle des Algues. Un problème intéressant serait de savoir pourquoi celles des *Chlorophycées*, à partir du même point de départ, et bien qu'elles aient manifesté parfois les mêmes tendances, ont dans l'ensemble évolué tout autrement que celles des *Chromophycées*.

G. F. PAPENFUSS (Berkeley, Calif.)

Problems in the Classification of the Marine Algae

A review is given of the present systems of classification of the green, brown and red algae and the bases upon which they are established.

Chlorophycophyta

Method of reproduction and life histories are of importance in the delimitation of certain orders, but somatic organization plays a more important rôle in the division of this phylum into orders. It is now fairly well established that the same type of life history (e.g., alternation of isomorphic generations) has arisen independently in different lines of development.

The system of classification of the green algae presented at this time (Fig. 1) departs in certain major respects from those currently followed. This system combines certain features of the systems of FRITSCH and SMITH and incorporates

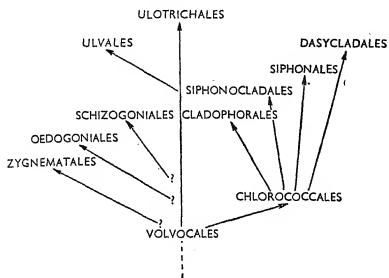


Fig. 1. Diagrammatic representation of the probable interrelationships of the orders of the green algae.

the unpublished conclusions of Miss EUBANK presented in a thesis at the University of California in 1949.

Phaeophycophyta

The system which is generally followed today is the one published by KYLIN in 1933. It is to a large extent based upon life histories.

The chief faults of this system appear to be that: 1. it excludes the *Ectocarpales* as the possible ancestral group of certain other orders, whose less advanced members possess many of the features of the *Ectocarpales*; and 2. it obscures the fact that polystichous forms are well represented in the Isogeneratae also. The arrangement to be presented now (Fig. 2) is one in which the *Ectocarpales* (*sensu limit.*), in agreement with the opinion of FRITSCH and others,

constitutes the basic group from which have evolved several phyletic lines.

Rhodophycophyta

A new era in the classification of the class *Floridæ* started in 1923 when KYLIN refined the ideas of SCHMITZ and produced a system based on the auxiliary cell. This system reached its culmination in 1932 in his paper on the order *Gigartinales* and has been in general use since that time.

The modified version of the system of KYLIN presented at this time takes cognizance of: 1. the occurrence of typical auxiliary cells, as they should perhaps be called, in some *Nemalionales*; 2. the existence of diplobiontic *Nemalionales*; 3. the occurrence of nutritive auxiliary cells in the *Gelidiales*; 4. the development of the gonimoblast from an ooblast filament in certain *Cryptonemiales* and *Gigartinales*; and 5. the development of the gonimoblast from an auxiliary cell situated in the carpogonial branch in certain *Cryptonemiales*, as recently established by Mrs. ABBOTT in her as yet unpublished thesis presented at the University of California in 1950.

A more detailed account is published in *Svensk Bot. Tidskrift* 45, 1951 p. 4-11.

H. SKUJA (Uppsala)

Phylogenetische Stellung der Glaucophyceen

Es gibt nur noch wenige von den niederen Organismen, die ein ebenso wechselreiches Schicksal in der Systematik gehabt haben wie die Glaucophyceen. Sie umfassen die weit bekannten Gattungen *Glaucocystis* und *Gloeochara*, sowie einige andere zur Zeit noch wenig erforschte Typen. Ihrer Farbe wegen anfangs als Blaualgen betrachtet, wurden sie sodann zu den Bangioideen geführt oder auch als eigentümliche Grünalgen aufgefasst; in der neuesten Zeit, im Anschluss an die Symbiose-Theorien der Zelle einiger früheren Forscher, ist die Frage nach einem besonderen symbiotischen Typus hier in den Vordergrund gestellt.

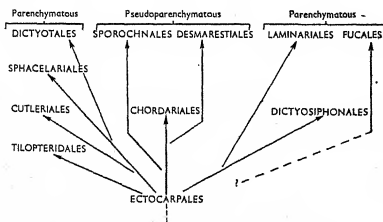


Fig. 2. Diagrammatic representation of the probable interrelationships of the brown algae.

Offensichtlich vertreten die Glaucophyceen eine besondere Gruppe sui generis von niederen algoiden Organismen.

Es bleiben dabei besonders zwei Möglichkeiten übrig: 1. Sie sind als symbiotische Formen und zwar als Endosyncyanosen (PASCHER) zwischen chroococcoiden Blaualgen und irgendwelchen apochromatischen algoiden oder monadoiden Organismen aufzufassen, oder 2. sie stellen die Überreste einer phylogenetisch uralten Übergangsgruppe zwischen den Blaualgen und Grünalgen dar.

Für die erste Annahme spricht gewissermaßen der Umstand, dass man recht viele Fälle von Symbiosen zwischen Blaualgen und verschiedenen farblosen niederen Organismen kennt und die Glaucophyceen-Chromatophoren, wie das besonders GETTLER gezeigt hat, in ihrem Aufbau grössere Ähnlichkeit mit einer Blaualgenzelle aufweisen. Als die vermutlichen farblosen Komponenten werden dabei gewöhnlich (GETTLER, PASCHER) einige apochromatische Tetrasporalen gedacht. Letzteres scheint mir jedoch aus mehreren Gründen sehr fraglich zu sein. Und zwar kennen wir erstens keinen Fall von dem Auftreten solcher relativ hochstehenden farblosen Tetrasporalen in der Natur; zweitens, sollte das auch einmal geschehen, so scheint es wenig wahrscheinlich, dass so verschiedene tetrasporale Formen unabhängig voneinander die symbiotischen Blaualgen irgendwie bekommen haben; drittens, das Besiedeln der hypothetischen Tetrasporalen konnte nur im Schwärmerstadium geschehen, doch bilden nicht alle Glaucophyceen mehr bewegliche, nackte Vermehrungskörper aus, z. B. *Glaucocystis*, welche übrigens mehr an die autosporinen Oocystaceen erinnert. Das Zustandekommen der Glaucophyceen-Symbiose muss allem Anscheine nach phylogenetisch sehr frühzeitig, in einem Stadium, wo die apochromatische Komponente sich noch im monadoiden Zustand befand, zurückgelegt werden. Die Glaucophyceen — mögen sie auch als symbiotische Gruppe betrachtet werden — sind phylogenetisch vermutlich recht alt und die Ausbildung von tetrasporalenähnlichen Formen bei ihnen ist

offenbar unabhängig, als konvergente Erscheinung oder homologe Entwicklungsreihe, zustande gekommen. Meine Beobachtungen über die Schwärmer von *Gloeochaete*, die nicht radiär sondern dorsoventral gebaut und mit zwei ungleichen Geisseln versehen sind, sprechen ebenso dagegen, dass die apochromatische Komponente hier eine Tetrasporale sein könnte. Eher handelt es sich bei den Glaucophyceen um eine gesonderte von irgendwelchen dorsoventral gebauten Protoblepharidineen oder anderen farblosen Flagellaten herstammende syncyanotische Entwicklungsreihe, die selbständig zu einem zellulären Stadium vorgeschritten ist.

Immerhin soll auch die andere Möglichkeit, dass es sich bei den Glaucophyceen um das Überbleibsel einer uralten Übergangsgruppe zwischen den Blau- und Grünalgen handeln könnte, nicht ausser Acht gelassen werden. Dabei könnten die eigenartigen Assimilationsplastiden der Glaucophyceen als noch unvollständiges Differenzierungsprodukt aus dem Chromatoplasma, ihr Zellkern als ein Derivat des Zentroplasmas mit ihrem Chromidialapparat aufgefasst werden. An eine solche Möglichkeit habe ich besonders am Anfang meiner Studien über die Glaucophyceen gedacht; nachdem ich die abgeleiteten Schwärmer von *Gloeochaete* jedoch kennengelernt habe, scheint mir die Annahme für die Gruppe einer symbiotischen Herkunft besser begründet. Allerdings, wie hervorgehoben, kann es sich dabei nicht um eine phylogenetisch junge, von irgendwelchen rezenten Tetrasporalen und Chroococcalen herstammende Gruppe handeln. Höchstwahrscheinlich vertreten die Glaucophyceen eine geologisch recht alte Gruppe symbiotischer Organismen, die als solche eine weitgehende phylogenetische Entwicklung von monadosyncyanotischen zu tetrasporalenähnlichen Formen durchgemacht haben.

Von diesem Standpunkt ausgehend, erscheint mir die Absonderung der, obschon recht kleinen, Gruppe der Glaucophyceen zu einem besonderen Pflanzenstamm der *Glaucophyta* taxonomisch wohl begründet und systematisch zweckmässig. Es bleibt noch zu untersuchen, ob einige glauco-

phytenähnliche Formen doch nicht Vorfahren der Grünalgen etc. gewesen sind.

O. JAAC (Zürich)

Über die Variabilität einiger Cyanophyceen unter dem Einfluss der Umweltbedingungen

Vielfach begegnet die Identifizierung von Blaualgen, sowohl aus dem Formenkreise der *Chroococcales* wie auch der *Hormogonales* beinahe unüberwindlichen Schwierigkeiten. Dies liegt begründet einerseits in der mangelhaften Beschreibung vieler Arten, anderseits aber auch in der auffallend weiten Plastizität derselben in Abhängigkeit von den Umweltbedingungen, unter denen sie heranwuchsen. Dabei kommt der Belichtungsintensität, dem Benetzungsgrad und der Reaktion (pH-Wert) des Wuchsortes besondere Bedeutung zu.

Die Abhängigkeit der Wachstumsintensität (Fläche und Trockengewicht der Kolonie) und der Ausgestaltung des Thallus vom Lichtklima konnte experimentell klar festgestellt werden an Reinkulturen, die angelegt wurden durch die Isolierung (mittels des Mikromanipulators) wenigzelliger Hormogonien eines Materials, das der Art *Tolypothrix distorta* var. *penicillata* (Ag.) LEMM. einermassen entsprach. Eine Kolonie, die sich aus einem wenigzelligen Hormogonium entwickelt hatte, wurde in 50 Erlenmeyer auf sterilen Erd-Agar übergeimpft. Diese Kulturen wurden in 5 Serien (in 10-facher Wiederholung) einer unterschiedlichen, von Serie 1 bis Serie 5 zunehmenden Belichtung ausgesetzt, die (in Lux-Stunden ausgedrückt) aus nachstehender Tabelle ersichtlich ist.

<i>Scytonema polymorphum</i> ; nova sp. in Abhängigkeit von Lichtgenuss				
Serie	Verhältnis im Lichtgenuss	Summe in Lux-Stunden	Mittlere Fläche der Kolonie	Mittleres Gewicht in mg.
1	1	52 000	1	1
2	2,5	130 000	12	5
3	7,5	390 000	69	13
4	73,0	3 800 000	160	108
5	136,0	7 100 000	126	69

Es ergaben sich Kulturen, die innerhalb der einzelnen Serien nach Grösse und Habitus nur sehr wenig variierten, während sie von Serie zu Serie in auffallendem Masse verschieden waren: Serien 1–3 frisch dunkel grün-blaue Koloniefarbe, Serien 4–5 Kolonien braun-grün. Die mittlere Fläche und das mittlere Gewicht der Kolonien (aus je 10 Wiederholungen) sind aus Kolonnen 4 und 5 der Tabelle ersichtlich.

Besonders eindrucksvoll sind nun aber die Unterschiede in der Ausgestaltung des Thallus, d. h. der Trichome und Fäden, unter dem Einfluss der unterschiedlichen Belichtung. Nachstehende Tabelle gibt diese Verhältnisse in übersichtlicher Darstellung wieder. Halten wir insbesondere folgende Tatsachen fest:

Versuchsreihe	Fadenverzweigung		Heterozysten	Farbe der Trichome	Farbe der Fadenscheiden	Beschaffenheit der Scheidenoberfläche
	einfach	doppelt				
5	keine	sehr reichlich	sehr reichlich	braun-grün bis gelblich	gelb-braun	rauh
4	keine	reichlich	sehr reichlich	braun-grün bis gelblich	gelb-braun	rauh
3	spärlich	ziemlich reichlich	spärlich	blau-grün bis grün-braun	farblos	glatt
2	spärlich	keine	keine	frisch blau-grün	farblos	glatt
1	sehr spärlich	keine	keine	frisch blau-grün	farblos	glatt

1. Farbe der Trichome: frisch blau-grün in den einer geringen bis mittleren Belichtung ausgesetzten Serien (1–3); braun-grün in den stark belichteten Serien (4–5).

2. Beschaffenheit der Scheiden-Oberfläche: glatt bei schwacher Belichtung; rauh (körnige Ausscheidung) bei starker Belichtung.

3. Pigmentierung der Fadenscheiden: fehlend in den Serien 1–3; deutlich braun in den Serien 4–5.

4. Heterocystenbildung: fehlend in den Serien 1-2, spärlich in Serie 3, sehr reichlich in den Serien 4-5.

5. Art der Scheinverzweigung: Im schwachen Licht (Serien 1-3) ist die Bildung von Fadenverzweigungen gering; alle Scheinverzweigungen sind „einfach“. Bei starker Belichtung (Serien 4-5) bilden sich reichlich Scheinverzweigungen; sie sind immer „doppelt“.

Dieser Art der Variabilität trägt nun die heute geltende Gattungs- und Art-Systematik in ungenügendem Masse Rechnung. Zweifels- ohne sind in manchen „Arten“ Entwicklungszustände festgehalten als der Ausdruck der Umweltbedingungen, unter denen das Material, das bei der Erstbeschreibung vorlag, heranwuchs. Wenn einmal eine grössere Zahl von Umweltfaktoren auf das von uns untersuchte Material experimentell geprüft sein wird, dürfte sich eine noch viel weitergreifende Plastizität der Art nachweisen lassen.

Was ist nun aber bei unserm Material (das sich unter keiner Artdiagnose unterbringen lässt) konstant, d. h. was ist von der Belichtungsintensität unabhängig? Die variationsstatistische Bearbeitung der Zell- bzw. Trichombreite ergab für das Freiland-(Ausgangs-)Material einen Mittelwert von $10,49 \mu$ und eine Streuung von $\pm 0,66 \mu$. Die Trichombreite der 200 ausgemessenen Fäden schwankt also am Freilandmaterial auffallend wenig. Desgleichen auch die Trichombreite des unter verschiedenen

starker Belichtung herangewachsenen Kultur-Materials. Die Mittelwerte der Trichombreite liegen bei den 5 Lichtserien zwischen den Werten von $10,05$ und $10,69 \mu$, variieren also nicht viel mehr als ein halbes μ , woraus sich ergibt, dass die Zell-, bzw. Trichombreite ein zuverlässig verwendbares Merkmal einer Art darstellt.

Eine ähnliche Plastizität ist vom Verfasser in früheren Arbeiten für Vertreter anderer Formenkreise nachgewiesen worden. So insbesondere für *Gloeocapsa sanguinea* (Ag.) Kütz. hinsichtlich der Pigmentierung und Ausweitung der Gallerthüllen in Abhängigkeit vom pH-Wert und Benetzungsgrad des Wuchsortes, sodann für *Scytonema myochroux* (DILLW.) Ag. — *Petalonema alatum* BERG. hinsichtlich der Ausgestaltung der Fadenscheiden. In allen diesen Fällen, aber auch im Formenkreise der Oscillatoriaceen erwies sich die Trichombreite (Zellbreite) als ein sehr weitgehend konstantes und von den Umweltbedingungen unabhängiges Merkmal.

Auf solche Verhältnisse wird die Gattungs- und Art-Systematik bei den Cyanophyceen inskünftig in stark vermehrtem Masse Rücksicht nehmen müssen.

Da das untersuchte Material sich in keiner bisher aufgestellten Artdiagnose unterbringen lässt, seine Plastizität aber noch nicht in genügendem Masse abgeklärt werden konnte, wird die bearbeitete Blaualge vorläufig bezeichnet als *Scytonema polymorphum* nov. sp.

SESSION 7

July 18th, 1—5 p. m.

Chairman: F. E. FRITSCH, Recorder: H. SKUJA

SUBJECT:

Algae: Phytogeography

W. R. TAYLOR (Ann Arbor, Mich.)
*Marine Algal Vegetation of the
 Marshall Islands in Comparison with
 Other Tropical Areas*

In 1946 six months were spent in a field study of the plants of Eniwetok, Bikini, Rongelap, and

Rongerik Atolls. Eniwetok Atoll is somewhat isolated from the others by distance and deeper water, but all are very similar. They lie in the path of the westward tending North Equatorial Current at 12° N. L. They each show an interrupted ring-like reef flat with a raised seaward margin and small, low islands. The raised reef

margin on the windward side is usually spectacularly pink and is composed of *Porolithon*; that on the leeward side is mostly composed of corals. The beach sand and rock is composed of Foraminifera as well as fragments of the Lithothamnium and corals. The lagoons support a rather simple flora with nothing about the margin especially characteristic except a little *Laurencia*, but the general lagoon floor supports, together with corals, a heavy flora of *Caulerpa* and *Halimeda*, to the extent that the segments of the latter are at least as important as the coral and shell fragments in contributing to the bottom sediments. These same elements have recently been shown by geologists to have been building up these atolls for a considerable geological period, and the rock composition corresponds closely to that found at Funafuti in the Ellice Islands.

The total marine flora at these Marshall Islands is about 150 species. In addition to the dominant elements of the reef and lagoon certain other things are noteworthy. Generally over the reef, but especially on the ridge, there is a good deal of *Pocockiella variegata*. Chiefly on rocks or boulders near the islands, or emergent reef areas away from the surf, there may be much *Microdictyon*. Over the level smooth reef flat algae may be scarce or represented by a close turf of *Centroceras*, *Jania*, etc., with *Neomeris* and *Liagora*. In deep channels and cavernous pools communicating beneath the reef with the sea there is a rich growth of *Halimeda*, *Udotea*, and *Caulerpa*.

The most similar floras elsewhere reported come from small islands and atolls. Since none have been exhaustively studied we can only say that partial similarities occur in accounts from the Caroline, Gilbert, and Ellice Islands. On the other hand the larger islands, especially at Tahiti, Samoa, Hawaii, Indonesia, and the Philippines, show much more diversification. The flora has most in common with that of Malaya and Polynesia, especially the former, but differs from the floras of these regions in having about twice as large a proportion of Chlorophyceae. This is compensated for by a

somewhat lower proportion of Rhodophyceae and especially of Phaeophyceae, from which Sargassa are absent. There is no marked American or Caribbean element.

E. Y. DAWSON (Los Angeles, Calif.)

On the Correlation of Marine Vegetation with Upwelling along the Pacific Coast of Baja California, Mexico

Studies of the intertidal algae of the Pacific Coast of Baja California, Mexico, have shown that to the south of the United States boundary a marked change occurs in the ratio of species of northern and of southern facies. The prevalence of characteristically cold-water elements along this coast and their proportional increase in the flora for nearly 300 miles to the south of La Jolla, California, where a relatively warm-water flora is well known, have indicated a reversal in the normal latitudinal temperature trend. In order to investigate the temperature situation and better to relate the distribution of the intertidal algae to the marine climate, a survey of these coastal waters has recently been carried out using a recording hydrothermograph for surface temperatures and a bathythermograph for subsurface temperatures. The survey has shown conclusively the occurrence of upwelling of cold, subsurface water along the greater part of the peninsular coast. The upwelling is most intense to the south of prominent headlands. Minimum temperatures, indicating regions of maximum upwelling were obtained in the areas south of Cabo Colnett at latitude $30^{\circ} 55'$, Punta Baja at latitude $29^{\circ} 55'$, Punta San Roque at latitude $27^{\circ} 10'$ and Punta Entrada at latitude $24^{\circ} 30'$. The presence of upwelling was found invariably to be accompanied by an increase in the luxuriance of the flora, and nearly always by the occurrence of beds of *Macrocystis*. A comparison of the flora of Isla Guadalupe with that of the peninsular coast at the same latitude demonstrates clearly the effects of the cold upwelling water in counteracting the normal latitudinal temperature trend.

M. WÆRN (Uppsala)
*Pictures of Brackish Algal Vegetation
 of the Baltic*

A successively pauperized offshot of the rocky shore algal population of the Atlantic extends into the Baltic. Numerous species stop at different points in the transitional areas to the Baltic, which are characterized by an instability in the salinity of the water and by a rapid fall from 30‰ to 10‰ in salinity within a comparatively short distance, viz. 300–400 km from Skagerrak in the north to the narrow sounds between Sweden, Denmark, and Germany in the south. Characteristic of the Baltic itself is the stability in the salinity of the water, slowly falling from 10‰ to fresh water from the south to the north within a long distance of 1500 km. Several large, partly dominant, algae such as *Ascophyllum nodosum*, *Halidrys siliquosa*, *Laminaria digitata*, do not enter into the real Baltic east of the German Belt Sea; and *Laminaria saccharina*, *Delesseria sanguinea*, and *Phycodrys sinuosa* cease to play a part east of Bornholm. *Fucus serratus* ceases at Gotland and *Rhodomela subfusca*, which is prominent still north of Gotland, ends half-way up in the Baltic.

This sapping of species yields more space to those remaining in the vegetation as well as to meeting lacustrine species and to *Sphacelaria arctica*, an arctic species isolated in the Baltic. On the rocky shores in the Öregrund Archipelago (north of lat. 60°), the following belts with dominating species were shown on submarine photographs.

A. In the Åland Sea:

1. *Fucus vesiculosus* belt between low water mark and about 10 m depth: *Ceramium tenuicorne* with *Lithoderma subextensum*, *Pylaiella rupicola*, *Fucus vesiculosus* with *Rhodochorton* and *Hildenbrandia*, *Cladophora rupestris*, *Furcellaria fastigiata*, all mentioned in the order in which they dominate, sometimes in zones, from the water surface down.

2. *Sphacelaria arctica* belt between 10 m and 22 m depth: *Furcellaria fastigiata*, *Rhodomela*

subfusca, *Polysiphonia nigrescens*, and *Sphacelaria arctica* and *Lithoderma Rosenvingii*.

B. In the Bothnian Sea:

1. *Cladophora* belt between low water mark and about 9 m depth: Diatoms, *Cladophora glomerata*, *Cladophora aegagropila*, and *Fontinalis dalecarlica*. In its deeper half, a relic of the *Fucus* belt is found.

2. *Sphacelaria arctica* belt from about 9 m down to the end of vegetation: *Furcellaria fastigiata*, *Polysiphonia nigrescens*, and *Sphacelaria arctica* with *Lithoderma Rosenvingii*.

E. TEILING (Linköping)

*Phytoplanktic Associations of Swedish
 Lakes*

The lecturer, by way of introduction, gave a short historical survey of the phytoplanktonic research in Sweden before 1911, when he began his investigations. He soon found the two principal types of phytoplankton, then known and discussed, viz. the Baltic type studied especially in Germany and Denmark, and the Scottish type. The former type is characterized by protococcoid and blue-green algae often in high-production, the latter is differentiated by its richness in desmids and lack of blue-green water-flowering. The impossibility of combining these types was then a problem much discussed but not solved by limnology. Finding these types side by side in adjacent lakes the lecturer was able to state that the difference was of ecological nature and due to the nutritive substances of the actual lakes. The water of rocky basins in archæan bedrock contains a small amount of nutritive substances and has a planktonic vegetation, small in quantity but, qualitatively, rich in desmids. With increasing proportion of nutritive substances in basins surrounded by clay and cultivated soil and settlement the planktonic protococcoid and blue-green algae are favoured and often form high-production whilst the desmids decrease. In view of the fact that the Scottish type was found also in Norway and Sweden the lecturer then called it the Caledonian type, the geolog-

Oligotrophy—Mesotrophy—Eutrophy



ical Caledonian faulting region being common to Scotland and Scandinavia.

This explanation was adopted by NAUMANN and the two types are now known as oligo- and eutrophical. The lecturer emphasized his priority in this explanation, published already in 1916 in a paper "En kaledonisk fytoplanktonformation" (Svensk Bot. Tidskr.), unhappily written in Swedish and owing to certain circumstances not referred to by the Swedish limnologists of that time.

On the basis of investigations of about 600 lakes of the southern third of Sweden the lecturer had been able to erect a continuous series of phytoplankton associations, covering the planktonic spectrum of these lakes from the most oligotrophical up to contaminated ones. The main groups of associations are those of *Desmidiata*, *Protococcaleta*, and *Myxophyceta*. As boundary marks of the secondary associations the lecturer uses certain stenotrophical leading forms, the presence or abundance of which characterizes the type of association. Most of the phytoplanktonic forms are eurytrophical occurring in lakes of diverse trophy. Especially in the case of the stenotrophical forms the optimal degree of their trophy is indicated by their abundance and the minimal degree by their stunted growth.

The leading forms are the following, from the oligotrophical towards the eutrophical end of the planktonic spectrum: *Dactylococcus ellipsoideus*, *Tabellaria flocculosa* var. *pelagica*, *Kriegerella lunaris*, *Fragilaria crotonensis*, *Achnanthes zachvatkini*, *Melosira granulata*, *Microcystis aeruginosa*, *M. viridis*, and (in Southern

Scania, on mesozoic ground) *Lyngbya contorta* and *Pediastrum kawrauskii*. The lecturer submitted lists of the most prominent characteristic forms of the main associations as well as a list of eurytrophical forms.

In the above chart is shown the trophical series of the main types of Swedish phytoplanktonic associations and the leading forms mentioned above and also some subordinate leading forms. The intimate dependence on the ground and soil is visible in the corresponding section of the country. The "limit of sedimentation" means the upper limit of clay sedimented in the sea and ancient ice-lakes.

F. E. ROUND (Liverpool)

The Ecology of the Algae of Some Littoral Sediments of Some English Lakes

The presence of an algal flora colonising the littoral sediments of these lakes has been known at least since 1933-5 as the result of Dr. GODWARD's investigations.

Since then, improved sampling techniques have been devised (LUND 1942) and have made possible a more detailed ecological survey of these algae.

Extensive sampling has shown this flora to be comparable in species and numbers per count at 15 stations on both Windermere North Basin and Blelham Tarn. Lakes of different types have, however, yielded quite a different range of species and numbers per count.

Continuous sampling over a period of 20 months has enabled the author to form a more accurate picture of algal growth than has hitherto been possible. Qualitatively, the flora has been shown to be extremely diverse with an especially large number of Diatoms and Cyanophyceae. Quantitatively, the population shows a Spring-Early Summer Maximum of Diatom growth, followed by a fall in numbers during July, a secondary small maximum in September, followed by extremely low numbers in November. After this, the population slowly recovers during winter and may have a subsidiary peak in January, e.g. Windermere.

The Cyanophyceae follow a similar curve in Windermere where they are high in numbers during the period March–June, and low for the rest of the year. The results for Blenheim are similar but its maxima and minima are never so high or low as those of Windermere.

If graphs are constructed for the component genera and species, a very similar seasonal sequence is revealed with minor specific variations.

Depth transects down to 12 m, carried out throughout the period, show that there is virtually no growth below 6 m, and even before this, the numbers are beginning to decline.

From these two sets of data, it would appear that light and temperature (the latter to a lesser extent) condition the seasonal cycle, and superimposed on this are the effects due to depletion of nutrients and disturbances (by storms, etc.) of the littoral deposits.

In contrast to the plankton, it is noteworthy that the bottom-living species have never been observed to be affected by *Chytrid* epidemics.

C. CEDERCREUTZ (Helsingfors)

Felsenalgen in Fennoskandien

Im Jahre 1941 veröffentlichte ich eine kleine Studie über die Felsenalgen in Finnland. Diese Studie gründet sich fast ausschliesslich auf Untersuchungen, die in den südlichen Teilen dieses Landes ausgeführt wurden. Seitdem habe ich vergleichende Studien in den Gebirgsgegenden in Nordfinnland sowie im nördlichen Schweden (Torne Lappmark und Jämtland) betrieben. Möchte jetzt in grösster Kürze die Resultate meiner Untersuchungen besprechen. (Die Diatomeen kommen hier nicht in Betracht.)

Beim Überblicken meines Materials geht es deutlich hervor, dass die Felsenalgenvegetation in Finnland und wahrscheinlich im ganzen Fennoskandien sehr gleichartig ist. Die ersten Besiedler der Felsen sind wie in anderen Ländern die Chroococcaceen und Nostocaceen, und wenn diese ihre schleimigen Lager ausgebreitet haben, finden sich die Stigonemataceen und

Scytonemataceen ein. Als Pioniere können auch *Phormidium*-Arten und *Coccomyxa* auftreten. Besonders allgemein scheinen an unseren sauren Granitfelsen *Gloeocapsa magma* und *Gl. montana* zu sein. *Gloeocapsa alpina* scheint charakteristisch für basische Felsen zu sein. Es scheint mir als wären mehrere *Gloeocapsa*-Arten für kennzeichnend. Die *Nostoc*-Arten dürften an die Algenvegetation der kalkhaltigen Felsen basischem Gestein reicher entwickelt sein als auf saurer Unterlage. Die Stigonemataceen und Scytonemataceen sind durch mehrere Arten vertreten. Oft kommen einige zusammen vor. Ein wichtiges Felsenelement ist auch *Synechococcus aeruginosus*. Die sehr nahestehende, etwas grössere Form, *S. major*, habe ich zwar auch an Felsen angetroffen, aber sie ist entschieden häufiger in Sümpfen.

Ein besonderes Interesse bietet die Desmidiaceen-Vegetation der Felsen, die in feuchten Moospolstern auftritt. Allgemein verbreitet sowohl in Nord- als Südfinnland ist *Mesotainium chlamydesporum*, ein Kosmopolit. Eine sehr bemerkenswerte Gruppe unter den Desmidiaceen bilden die sog. arktisch-alpinen Arten. Von ihnen habe ich 28 Arten an den Felsen angetroffen. Sie sind weitverbreitet im hohen Norden an verschiedenartigen Standorten. Einige von ihnen wie z. B. *Cosmarium cyclicum* v. *arcticum* und *C. speciosissimum* habe ich nur in Nordfinnland angetroffen, die meisten aber auch in Südfinnland, dort jedoch nur an Felswänden. Die Eigenart der Felsenalgenvegetation ist also deutlich mehr ausgeprägt in den südlicheren als in den nördlicheren Teilen von Fennoskandien. Die zufälligen Elemente, die von verschiedenen Gewässern herkommen, sind an den Felsen der nordischen Gebirge auch zahlreicher als in den südlicheren Gegenden mit ihren mehr oder weniger isolierten Felswänden. Mit den Schmelzwasserbächen folgen selbstverständlich viele Algen von den Gebirgssümpfen mit und verbreiten sich an den Felswänden.

Discussion

W. VISCHER: Wie der Autor erwähnt, und wie andere Autoren erwähnt haben, werden in

Algenlisten sehr oft „Sammelarten“ aufgeführt. Solche Arten „können über die Ökologie des Standortes nichts aussagen“ (z. B. *Hormidium*-Arten). Werden aber von verschiedenen Fund- und Standorten solche Sammelarten in Kultur genommen, so zeigt es sich, dass sie aus sehr verschiedenen Arten oder Rassen bestehen, von denen jede besondere Ansprüche auf den Standort stellt. Arten von *Hormidium* sind z. B. sehr verschieden in ihren Ansprüchen auf die Reaktion (pH) der Unterlage. Wenn mehr solche steno-oecischen Rassen genauer unterschieden werden, dürften Algenlisten als ökologische Anzeiger an Wert wesentlich gewinnen.

A. A. ALEEM (Alexandria)

Ecology of Marine Littoral Diatoms

The investigation deals with the principal features of distribution and ecology of littoral diatoms inhabiting certain localities both on the south coast of England and on the west coast of Sweden. The distribution of the species varies with such factors as salinity, type of substratum, height above chart datum, and season.

Two chief communities are characteristic of the 'spray zone' both in England and Sweden, viz. *Achnanthes brevipes*, blue green, and *Amphipleura rutilans*. The former occurs on sloping rock-surface, while the latter in supralittoral pools and ditches. Species like *Rhabdonema arcuatum*, *Grammatophora marina*, *Rhoicosphenia marina*, and *Achnanthes longipes* tolerate more submergence than exposure. Certain species are more sensitive to changes of salinity than others.

The periodic development of some littoral diatoms was followed and emphasis has been laid on the part played by such diatoms in the colonisation of the substratum.

N. QUENNERSTEDT (Uppsala)

On the Diatoms of Swedish Mountain Lakes

Few, if any, diatom species deserve the epithet of "mountain" or "alpine", as practically

all species found in the mountains also are known in the lowlands.

However, certain types of algal communities, where diatoms play a rôle, seem to be characteristic of mountain waters.

In the North-Swedish province of Jämtland the river-basin of Långan¹ gives examples of lakes with a very specific algal vegetation, due to habitat conditions, which are extremely different from those of known lowland waters.

The lakes at lower altitudes of the Långan system—about 318–335 m above the sea-level—represent however a more ordinary oligotrophic type with *Isoteles lacustris*, *Lobelia dortmanna*, and a diatom flora relatively rich in species. The waters have a slightly acid reaction (pH 6.5–6.8) and a specific conductivity of $\kappa_{18} = 12$ –16. The Ca content is low (about 1–1.66 mg/l).

At higher altitudes some of the lakes are exceptionally poor in dissolved mineral substances, and the specific conductivity is very low. The lowest conductivity found is $\kappa_{18} = 4$. Example: Resemejaure, 922 m above the sea-level: pH 6.1; 0.16 mg Ca per l.

Broadly speaking, there is a certain correlation between the decreasing concentration of cations and the number of diatom species in the lakes. Thus only a few species are present in lake Resemejaure and, moreover, the diatom vegetation is altogether very scanty in this lake, where blue-green algae are predominating in the benthic vegetation.

An intermediate state between the extremely poor type of Resemejaure and the more common oligotrophic lakes is represented by Övre Oldsjön (582 m above the sea-level; $\kappa_{18} = 8$; pH 6.1–6.2; 0.24–0.50 mg Ca per l). Here the diatom vegetation (and the Cyanophyceae, too) is quantitatively very rich. The following species of diatoms are locally abundant: *Anomoeoneis exilis*, *A. serians* v. *brachysira*, *Eunotia lunaris*, *Frustulia rhomboides* v. *saxonica*, *Peronia Heribaudi*, *Tabellaria fenestrata* v. *intermedia*, *T. flocculosa*.

The maximal occurrence of these species ex-

¹ The sources of Långan are situated about lat. 64° N., not far from the Norwegian frontier.

cept *Frustulia* is confined to relatively shallow water. *Frustulia* is forming mucous masses, especially on Cyanophyceae and mosses (*Blinidia*, *Marsupella*, *Polytrichum*). This *Frustulia* vegetation is generally best developed below the low-water line.

The fluctuations of the water level, the duration of submergence and emergence, are here factors of great ecological importance in determining the composition of the littoral algal vegetation.

Discussion

F. HUSTEDT:

Die ökologischen Faktoren sind komplexer Natur. Wir betrachten sie aber absolut, so

dass wir die tatsächliche Ökologie der Diatomeen-Arten nur schwer erkennen können. Die Temperatur ist als unmittelbarer Faktor nicht von wesentlicher Bedeutung, nordische Formen sind nicht ohne weiteres als stenotherme Kaltwasserformen zu bezeichnen, da sie oft erheblichen Temperaturschwankungen unterworfen sind. Massgebend ist der Chemismus der Gewässer. Bezüglich des Kalkgehalts handelt es sich nicht unbedingt nur um Calciumkarbonat, sondern allgemein um die hydrolytisch spaltbaren Karbonate. Die Wasserstoffjonen-Konzentration kann als unmittelbarer Faktor wirksam sein, wie sich aus dem Vergleich von humussauren Moorgewässern mit mineralsauren Gewässern ergibt.

SESSION 8

July 19th, 9 a. m. — 1 p. m.

Chairman: F. E. FRITSCH, Recorder: J. A. NANNFELDT

SUBJECT:

Algae: Development etc.

MARY A. POCKOCK (Muizenburg, C. P.)

Cell Division in the Volvocales and its Taxonomic Significance

1. In *Volvox* during asexual reproduction the gonidium undergoes successive divisions resulting in a hollow spheroid in which the nucleated species of the cells are directed *inwards*.

2. Hence completion of cell division must be followed by inversion before the cells attain their final orientation.

3. Similar phenomena are found throughout the *Volvocaceae* (sensu G. M. SMITH) not only in asexual reproduction but wherever a single cell divides to form a cell mass, i.e. in the formation of the male gametes and of the 'germ' colony formed on germination of the oospore.

4. Investigation of nuclear behaviour by the application of aceto-carminic methods in collaboration with Dr. MARION CAYE, gives a clear picture of nuclear behaviour.

5. Similar phenomena accompany division in the unicellular *Haematococcus* and *Chlorogonium*.

6. A different type of cell division is found in a small colonial alga, *Astrephomene gubernaculifera* from South Africa; in this, the nucleated apices of the daughter cells are from the first directed *outwards*; a different cell picture results and no inversion takes place.

Taxonomic significance: The differences in the type of cell division are regarded as fundamental; consequently the following modifications in the classification of the *Volvocales* are suggested:

1. A separate family, *Astrephomenaceae*, characterized by the outward position of the nucleus and consequent absence of inversion, is proposed, including at present only the one representative, *Astrephomene gubernaculifera*.

2. The family *Volvocaceae*, sensu G. M. SMITH, should be extended to include *Haematococcus*, *Chlorogonium*, and *Stephanosphaera*.

Further, in the case of unicellular algae, their behaviour during division may be taken as the chief criterion to determine their systematic position; in *Haematococcus* the cell continues motile throughout the process and the cell-picture conforms with that characteristic of the *Volvocaceae*.

On the other hand, the behaviour typical of *Chlamydomonas* where the cell comes to rest before dividing and the resultant cell-picture is quite different, may be regarded as characteristic of the family *Chlamydomonadaceae*.

Discussion

G. H. SMITH: Agreed in general with the proposed treatment of the colonial *Volvocales* but questioned the inclusion of *Haematococcus* and *Stephanosphaera* in the family *Volvocaceae*. Dr. Pocock was asked if *Haematococcus* and *Stephanosphaera* showed the characteristic cross at the eight celled stage, since this would seem to be a critical character for uniting them with the *Volvocaceae*.

MARY A. POCOCK: Nuclear picture in *Haematococcus* exactly comparable with that of *Volvox*.

P. DANGEARD: Chez le *Volvox aureus* les colonies-filles asexuelles se forment dans une colonie-mère ayant conservé sa motilité et leur sortie au dehors a lieu par effraction et rupture de la paroi de la colonie-mère.

R. A. LEWIN: A hollow sphere of cells, in which the nuclei are oriented towards the inner face of the sphere, can be found in the gametogenesis of *Chlamydomonas Moewusii*. In these respects this species resembles *Haematococcus*—of some interest in view of Miss Pocock's suggestions for a taxonomic revision in the *Volvocales*.

MAUD B. E. GODWARD (London)
Cytological Criteria in the Taxonomy of Spirogyra

The species of *Spirogyra* at the present time are delimited from one another essentially by the characters of the zygospore. This has meant

that when a species failed to form mature zygospores it could not certainly be identified. Since experimental material is usually in a vegetative condition, it is clearly advantageous to be able to identify it in this state.

Among the characters of the vegetative filaments are those of the dividing and resting nucleus. Twenty cytological photographs are shown to illustrate these. Four of the slides from which the photographs were made, are exhibited in the Cytology section and additional photographs shown there. These show that characters of taxonomic promise are:

in mitosis,

1. the number and size of chromosomes;
2. the length and position of the nucleolar-organising regions;
3. the kind of centromere organisation, diffuse or localised;
4. the distribution of the so-called "nucleolar substance";

in the resting nucleus,

1. the presence or absence of chromocentres;
2. the maximum number of nucleoli;
3. the different forms of the nucleolar-organising region in the nucleolus.

Especially interesting is the fact that no two species appear to be alike in both the number and size of the chromosomes, and their morphology. Evidence of diploidy exists in certain species. Under the circumstances it seems that if the taxonomy of the group were to include the cytological characters the result would be convenient and satisfactory. In *Spirogyra*, it is particularly easy to observe the cytological features by a simple rapid method published in my paper in the *Annals of Botany* 1950. At present I am engaged on counting the chromosomes of British species of *Spirogyra* and hope to publish a series of taxonomic papers including these numbers. In this work I am consulting with Professor F. E. FRITSCH regarding the taxonomy and have received valuable help from the staff of Natural History Museum, London, and the Herbarium, Kew. Since com-

ing to Stockholm I have also been given help in access to material at the Botanical Museum, Stockholm.

Discussion

J. W. G. LUND: As an ecologist I am most interested in this cytological method for identifying vegetative material of *Spirogyra*. I should like to ask if the methods used are simple enough to be suitable for those who are not cytologists. Further, does all material referable on morphological ground (*i.e.* on the characters of the zygote) to a given species, show the same chromosome structure and number; and vice versa?

MAUD GODWARD: In *Spirogyra* it seems improbable that there can be polyploid series as in the higher plants. There is no such a thing as a basic chromosome number for the genus, the number of chromosomes varying from 4 to 84 with numerous intermediate numbers. Probably polyploidy here is a totally different thing from what it is in the higher plants.

R. ROSS: Dr. GODWARD's investigations have provided us with a new set of morphological characters on which to base the taxonomy of *Spirogyra*, and one much more readily applicable to living material than the characters of the zygospore. The morphology of the nucleus is as much a morphological character to be considered in classification as the morphology of any other part of the plant. The difficulties this may bring to the interpretation of dried material in herbaria must be accepted. Advance in taxonomical science must not be retarded by the inadequate technique of our predecessors who had less knowledge than we now have.

LUCY B. MOORE (Wellington)
Oogamy in Sphacelariales

In five or six austral species of *Halopteris* antheridia and oogonia of characteristic form have been recognized. These gametangia match those described by SAUVAGEAU in the European *H. scoparia*. In *H. congesta* the discharge of the sperms and of the single large non-motile ovum has been observed, fertilization has been

watched, and embryos have been grown in culture. Similar embryos have been found adhering to sexual plants of this and two other species. In all oogamous species recognized there is an axillary cushion of cells, and the unilocular sporangia are borne in crowded clusters, in positions corresponding to those of the sexual sori. It is suggested that these reproductive characters may be common to all species that could rightly be included in KÜTZING's genus *Stypocaulon*, of which *H. scoparia* is the type. All these species have a fairly high degree of anatomical and morphological differentiation.

Two other southern genera, *Ptilopogon* and *Phloeocaulon*, showing even more vegetative complexity, are recorded by SAUVAGEAU as having two types of plurilocular sporangia, the compartments of the supposed female gametangia being twice as large as those of the supposed male. In *Phloeocaulon* two such types have been seen, but cultures have not been made. In *Ptilopogon* there is early division of the developing "gametangium" and individuals with compartments of various sizes may be seen close together; there has been no clear indication, however, in the few specimens seen, that the fully mature gametangia are of two kinds. Cultures so far have not been successful.

In *Cladostephus*, of comparable structure, SCHREIBER has shown that the gametes all look alike but belong to plus and minus strains that differ in behaviour. In none of these three genera does an axillary cushion of cells give rise directly to a crowded sorus of sporangia. Thus in *Sphacelariales* two trends may be seen, one towards vegetative complexity with only a small degree of differentiation of the gametes, the other towards oogamy with, as far as is known, a smaller amount of anatomical differentiation.

KATHLEEN M. DREW BAKER (Manchester)
Aspects of the Life History of
Porphyra umbilicalis (L.) Kütz.

Porphyra umbilicalis produces two types of spores, monospores and carpospores. In Eng-

land, the former appear to be rare and when found have occurred on thalli showing unusually sparse formation of carpospores. A single monospore is liberated from each mother-cell and germination has not been induced so far. Carpospores are formed abundantly and, when germinated in culture solution, form filamentous growths identical with those described by previous investigators. On the other hand, if germinated in contact with empty shells of molluscs or if the filamentous growths referred to above, are brought into contact with such shells or even egg-shells, the shell is penetrated rapidly and the resulting growth is soon identifiable as the shell-boring alga *Conchocelis rosea* BATTERS. This then explains how the species survives the period when absent from the littoral zone. *C. rosea* normally inhabits deep water but can be found in the intertidal zone.

Within three weeks of placing spores on sterile shells, infected areas are visible with a hand lens. These areas quickly increase in size and eventually extend to the other side of the shells. It is possible that denser growths are formed in cultivation than under natural conditions. The germ tubes which may penetrate the shell immediately beneath the spore or after growing to varying lengths, show sudden and marked changes at the point of entry. Irregularly growing, sparsely branched and occasionally septate filaments change to very straight non-septate filaments with a wealth of pinnate branches. In the external portion of the filament the plastids are parietal, ribbon-shaped and have an occasional pyrenoid but inside the shell they are diffuse and without pyrenoids. Fusions between branches of the same or neighbouring germlings are very frequent. At an early stage short swollen convoluted branches develop from the long straight filaments and ultimately a dense network fills the shell matrix. After a few months the structures, described as sporangia by earlier workers and consisting of rosettes of forked filaments growing more or less at right angles to the layers of the shell and to the vegetative filaments, develop in profusion. Their cells are

only slightly longer than broad and of much greater diameter than the vegetative filaments. Liberation of the contents, which are remarkable for a large central stellate plastid and pyrenoid, has not been observed.

Certain terminal cells of a number of such sporangia formed in a very small shell fragment have been found to push beyond the surface of the shell and develop into stubby filamentous growths, resembling figured germlings of *Porphyra* by their apical growth and by the shape and contents of their cells. In addition, disc-shaped structures (called plantlets) unattached in the later stages and just large enough to be visible to the naked eye, have developed in hollows of oyster shell matrix. The centre of the disc is densely parenchymatous and from it arise numerous filamentous projections, whose growth is apical. The contents of the cells is similar to those of the cells of *Porphyra*. Attempts to induce further growth of both the superficial structures and these plantlets have not yet been successful.

Discussion

P. DANGEARD: La découverte de Mme DREW est très intéressante pour moi étant donné que j'ai étudié autrefois le développement des carpospores des *Porphyra* (Volume jubilaire dédié à L. MANGIN). Dans l'interprétation de ce développement une difficulté paraît résulter du fait que le *Conchocelis rosea* est une algue de profondeur par exemple dans la région de Roscoff, tandis que *Porphyra umbilicalis* vit dans la zone littorale à faible profondeur.

S. SUNESON (Göteborg)

The Bisporo Problem in the Corallinaceae

In the absence of detailed cytological investigations no definite knowledge has so far been obtained as to the rôle played by the bispores in the life cycle of the Corallinaceae. Certain conclusions have been drawn from the size of the nuclei and from the presence or absence of sexual individuals in the bisporic species.

In order to elucidate the problem I have investigated two suitable species from the west coast of Sweden, viz. *Lithophyllum litorale* SUNESSON and *L. Corallinae* (CROUAN) HEYDR. For staining haematoxylin and the Feulgen reaction were used.

In *L. litorale* only bisporic plants are known. Neither tetrasporic nor sexual individuals have been met with. Therefore no reduction division could be expected. That was also verified by the cytological study. The chromosomes in the nucleus of the bispore-mother-cell were found to be unpaired in late prophase. Although a large material was studied no sexual plants and no normal tetraspores were found. In one crust I found a peculiar type of tetrasporangia with only two nuclei, just as in the bisporangia. These tetrasporangia seem to be equal to the normal bisporangia in cytological respect.

Lithophyllum Corallinae from northern waters was known to have sexual individuals and individuals with normal, uninucleate bisporangia. Tetrasporangia had only been met with in the Mediterranean. In spite of this the species was considered to have a regular alternation of generations also in the northern region and reduction division prior to the formation of the bispores. Studying a large material from Sweden I found normal tetraspores, though not frequent, intermingled with the bispores. Further, in some crusts I found bisporangia with four nuclei. These nuclei were distributed with two in each single bispore. Division stages of the spore-mother-cell were observed in many preparations. As a rule the chromosomes were unpaired in late prophase, just as in *L. litorale*. These stages are interpreted as belonging to the development of normal, uninuclear bispores. However, in a few preparations the nucleus was observed in an obvious stage of diakinesis with the haploid number of gemini. Here we are probably dealing with bisporangia developing four nuclei. Ripe bisporangia of that type were frequent in the conceptacles in question. Thus reduction division seems to precede the formation of the tetraspores and binucleate bispores in *L. Corallinae*. This opinion is also

supported by the size of the nuclei in the ripe spores, the uninucleate bispores having obviously bigger nuclei than the tetraspores and binucleate bispores. The two latter types of spores are supposed to give rise to the sexual individuals. The chromosome number was about 16 in sexual and 32 in asexual plants.

According to this investigation there seems to be no reduction division preceding the formation of the common, uninucleate bispores in the Corallinaceae.

My results have later been published in Bot. Not. 1950 pp. 429-450.

Discussion

G. F. PAPENFUSS: I should like to ask Dr. SUNESSON whether he has suggestions as to the distribution of the nuclei in thalli which develop from a binucleate bispore.

S. SUNESSON: In reply to Dr. PAPENFUSS's question about the behaviour of the binucleate bispores at their germination, I should say that it would of course be very interesting to try to let the spores germinate under controlled conditions to find out what sort of plants they may generate. Such an investigation must, however, be very difficult to perform, and so far we can only discuss this problem from a theoretical point of view. It is most likely that one of the nuclei disappears before the germination of the binucleate bispores.

G. M. SMITH (Stanford, Calif.)

Sexuality, Zygote Formation, and Zygote Germination in Chlamydomonas

Plus and minus clones of 15 heterothallic strains not fertile with one another have been isolated from soils from various parts of the United States. Species thus far identified among these strains are *C. minutissima* KORSCHIK., *C. intermedia* CHOD., *C. Reinhardii* DANG., and *C. Frankii* PASCHER. In addition 16 clones showing a homothallic sexual reaction have been isolated. All clones were cultured in an immobile palmelloid condition on nutrient

agar containing 0.2 % Beijerinck's solution and soil extract. Sexual reactions were studied after the cells had been made motile by flooding with water. In all strains gametic union was between vegetative cells and not between specially formed gametes. In two strains gametic union only took place between cells of small size; in all others between cells of any size. Cells must be cultured in a palmelloid condition for a certain length of time before they react sexually and, according to the species, this does not take place until the cultures are from three to fifteen days old. When sexually mature plus and minus cells are mixed they aggregate in clumps of 20 to 100 within five seconds and begin to fuse in pairs. Homothallic species begin to form clumps as soon as the cells become motile after flooding. Species with thick walls have an escape of protoplasts from the walls shortly after mixing motile cells of opposite sex. This could not be induced by placing motile cells of one sex in a filtrate from motile cultures of opposite sex. Unlike what has been reported for the *C. eugametos* group of species, all strains become motile and sexually functional in darkness. For *C. Reinhardtii* there is evidence that the sexual substances are formed in light, but that these are not the cis and trans crocetin mixtures as in the *C. eugametos* group. Zygotes of both hetero- and homothallic strains fall into the two following types: A) those in which all reserve food is contributed by the fusing cells, and B) those in which most of the food is due to photosynthetic activity of the zygote. Zygotes of type A are small and do not increase in size as they mature; those of type B become two to three times their original diameter. Both types of zygote must ripen for about 20 days before they are capable of germination. Germination of zygotes of most strains took place 24 to 72 hours after transfer to fresh nutrient agar. Germinating zygotes of all strains of type A produced four zoospores. Zygotes of some strains of type B regularly produced four zoospores, whereas those of other strains regularly produce 8, 16, or 32 zoospores.

Discussion

E. G. PREINGSHEIM: In *Polytoma* no shedding of cell-walls was ever observed, only those cells conjugating which have no cell-walls. Every gamete was able to multiply and so give rise to a population.

T. LEVRING (Göteborg)

Surface Layers of Unfertilized and Fertilized Eggs of Some Fucoids

By means of modern methods such as phase contrast and polarizing microscopy unfertilized and fertilized eggs of various fucoids (*Fucus* spp. and *Ascophyllum nodosum*) have been studied.

The surface of unfertilized eggs thus consists of the following layers: 1. A gelatinous coat stratified tangentially, which seems to be partly dissolved by the water; 2. the egg membrane, a very thin but distinct layer under the gelatinous coat. If distilled water is added to the eggs, they swell and often blisters are formed before they disintegrate. On the surface of these blisters the egg membrane is seen very clearly. It seems to be acting as an elastic membrane and plays an essential rôle in the formation of the fertilization membrane; 3. a plasma membrane containing lipid molecules arranged perpendicularly to the surface of the egg and tangentially arranged protein molecules; 4. a cortical layer (innermost), which produces material for building up the cell wall after fertilization. The surface of the egg shows a weak birefringence positive in radial direction.

The spermatozooids are surrounded by a thin gelatinous layer. Both the spermatozoid and the gelatinous layer contain polysaccharide sulphates, probably fucose sulphate.

After fertilization a cell wall is soon visible. If the eggs are plasmolysed by hypertonic sea water the wall is made plainly visible and the eggs do not disintegrate in distilled water. The cell wall consists of two layers: 1. The outermost is a remnant of the egg membrane (covered with the gelatinous coat) and 2. the innermost, which is increasing in thickness, shows a very strong birefringence negative in radial direction

and must therefore contain rod-shaped molecules arranged tangentially to the surface. It contains cellulose and polysaccharide sulphates. The strong birefringence is therefore certainly due to the occurrence of cellulose in the wall.

Contrary to unfertilized eggs the fertilized ones are stained metachromatically by toluidine blue. The staining is concentrated to the cortical layer of the protoplasm and the interior part of the wall. This staining is due to the occurrence of polysaccharide sulphates, at least partly fucose sulphate. The viscosity of fertilized eggs is higher than that of mature, unfertilized ones.

It is obvious that the cell wall formation involves a number of reactions in or close under the surface of the egg. The spermatozooids react with the surface and various enzyme systems are thereby released. In connection with this it may be mentioned that dupunol, a detergent consisting of a mixture of aliphatic long-chain alcohol sulphonates, has a blocking effect on the fertilization. The dupunol molecules are arranged on the surface, most likely in connection with the lipoid-protein membrane, and are thus blocking the reaction between the spermatozooids and the egg surface. If eggs are pre-treated with trypsin as a rule no cell wall is formed after fertilization.

At the fertilization cell-wall material is released in the periphery of the egg mainly in the cortical layer and is forced out through the plasma membrane. In some cases small con-

tractions in the surface have also been observed. This material reacts with the egg membrane, which is acting as a kind of templet supporter and the new wall is formed on the interior side of this membrane. After the fertilization the respiration of the egg also increases considerably.

Discussion

BETTY MOSS: The cell-wall structure of the Fucoids is a most interesting subject. Alginic acid or alginates are generally stated to be cell-wall constituents of the Brown Algae. Has their presence been detected in egg membranes or do they appear later in development?

T. LEVRIER: They are most likely present, but no microchemical test for alginates is yet known.

R. BAUCH: Die *Fucus*-Bestände, die in der Biologischen Forschungsanstalt Hiddensee untersucht wurden, bilden nur ganz selten Befruchtungsmembranen, keiner aber normal. Sind derartige Beobachtungen auch an schwedischen *Fucus* gemacht worden?

T. LEVRIER: Ähnliche Untersuchungen sind an der schwedischen Ostseeküste überhaupt nicht gemacht.

G. HYGEN: I should like to ask Dr. LEVRIER if the stratification of the gelatinous coat of the eggs, which he has observed, might be an optical artifact.

T. LEVRIER: The gelatinous coat cannot be an optical effect, as the coat separates eggs lying closely together.

SESSION 9

July 19th, 1—5 p. m.

Chairman: F. E. FRITSCH, Recorder: H. SKUJA

SUBJECT:

Algae: Varia

F. DROUET (Chicago, Ill.) and A. DAILY (Indianapolis, Ind.)

Revision of Coccoid Myxophyceae

Considerable field work and the study of some ten thousand specimens, including those in the

larger herbaria in North America and Europe and in many private collections, has shown that of the thousands of species, varieties, and forms described since Linnaeus, only about twenty-five autonomous species of this group exist throughout the world. These are all widely

distributed, each abundant in appropriate habitats in tropical and temperate regions, and some extending into the arctic and antarctic zones. The coccoid Myxophyceae have never been revised on the basis of studies of historical specimens, so that the species and genera in modern treatments are a product of repeated compilation and attendant misinterpretation of descriptions and illustrations. The type specimens of many of the described species have proved to be Chlorophyceae, flagellates, bacteria, fungi, protozoa, Rhodophyceae, spores of filamentous Myxophyceae, various organs of larger plants and animals, or inorganic bodies. Where the type specimens fall within the group, species have been transferred to numerous genera within the Myxophyceae and Chlorophyceae. It is expected that over three-fourths of the total number of type specimens concerned in the nomenclature of these so-called "unicellular" plants will have been found and studied during the course of this work. It is taken for granted that some may never have been preserved, that some have been destroyed in catastrophes, and that others are safely preserved in herbaria and private collections unknown or inaccessible to the authors.

F. HUSTEDT (Plön)

Parallelismus in der Strukturentwicklung verwandter Diatomeengattungen und seine Bedeutung für die Systematik

Die bisherigen Grundlagen für die Systematik der Diatomeen bilden die äussere Morphologie der Zelle und die Struktur der Zellwand. Mit dem Bekanntwerden neuer Arten wird die Systematik sowohl in Zoologie als auch Botanik besonders hinsichtlich der Umgrenzung der Gattungen immer schwieriger, und es muss fraglich erscheinen, wie weit noch das eine oder andere Merkmal zur Unterscheidung herangezogen werden kann, ausserdem lässt sich eine gewisse Inkonsequenz nicht verkennen. Bei den Diatomeen ist die Entwicklung besonders der Struktur der Zellwand in vielen Gattungen dieselben Wege gegangen, die aber nur zum

Teil zur Aufstellung neuer Gattungen führten. P. T. CLIVE zog 1894 aus der Gattung *Gomphonema* Ag. einige Arten heraus und schuf für sie die Gattung *Gomphoneis*. Als charakteristische Merkmale gibt er das Vorhandensein von Areolen-Doppelreihen zwischen den Transapikalrippen und von Längslinien beiderseits der Raphe an. Weitere Untersuchungen haben aber gezeigt, dass diese beiden Merkmale nicht miteinander gekoppelt zu sein brauchen, sondern nur den Grenzfall darstellen. Die Überprüfung anderer *Gomphonema*-Arten und die Auffindung neuer Formen ergibt für die Gruppe *Gomphonema-Gomphoneis* folgendes Bild:

1. Formen mit einfachen Poroidreihen, Längslinien fehlen.
2. Formen mit einfachen Poroidreihen, Längslinien vorhanden.
3. Formen mit Areolen-Doppelreihen, Längslinien fehlen.
4. Formen mit Areolen-Doppelreihen, Längslinien vorhanden.

Mit der Gattung *Gomphonema* ist die Gattung *Cymbella* Ag. nahe verwandt. Zu den bisher bekannten Arten mit einfachen Poroidreihen und ohne Längslinien fand ich Arten mit Areolen-Doppelreihen, teils mit, teils ohne Längslinien. Damit ergibt sich ein deutlicher Parallelismus in der Strukturentwicklung in beiden Gattungen. Es wäre verfehlt, die Zwischenformen als Vertreter neuer Gattungen aufzufassen. Offenbar handelt es sich nicht um qualitative sondern nur um quantitative Merkmale, die nicht zur Aufstellung neuer Gattungen herangezogen werden können. Der einzig mögliche Schluss, der aus diesen Beobachtungen gezogen werden kann, führt zur Kombination der Gattungen *Gomphonema* und *Gomphoneis* und zwingt uns gleichzeitig zu kritischer Prüfung eines jeden Merkmals, das für diagnostische Zwecke, insbesondere zur Aufstellung neuer Gattungen, ausgewertet werden soll.

Discussion

O. JAAG: Kann das Elektronen-Mikroskop etwas Neues für die Systematik zeigen?

F. HUSTEDT: Bei der Anwendung des Elek-

tronen-Mikroskops für taxonomische Fragen besteht die Gefahr, dass die Unterschiede, die wir insbesondere für Abgrenzung von Gattungen benutzen, mehr oder weniger verwischt werden. Im wesentlichen werden elektronenmikroskopische Studien uns mit dem Bau der Zellwand einzelner Arten bekannt machen, aber nur in kritischen Fällen für taxonomische Entscheidungen herangezogen werden können. Es muss dabei auf die Möglichkeit der praktischen Anwendung Rücksicht genommen werden.

R. W. KOLBE: Dr. HUSTEDTS Ansicht, dass man bei der Beurteilung von elektronenmikroskopischen Diatomeen-Untersuchungen sehr skeptisch sein müsse, hat er auf folgendes begründet:

1. Grosse Schärfentiefe des Elektronen-Mikroskops, daher Unmöglichkeit der Beurteilung räumlicher Verhältnisse.

2. Fehler durch Diffraktionserscheinungen.

3. Praktische Gründe (in der Systematik).

Entgegnung:

1. Räumliche Verhältnisse können leicht durch Stereoaufnahmen studiert werden.

2. Diffraktionserscheinungen sind beim Elektronen-Mikroskop sehr gering und praktisch zu vernachlässigen.

3. Elektronenaufnahmen sollen normal für kritisch-systematische und nicht für Bestimmungszwecke verwandt werden. Insbesondere haben elektronenmikroskopische Studien sich bereits bewährt für die Feststellung der Gattungszugehörigkeit zartester Formen.

R. ROSS: I am of the opinion that shape and symmetry have been given more weight than is proper in the taxonomy of diatom taxa up to the level of genera. I would suggest that the *Cymbella* shape, the *Gomphonema* shape, and probably also the *Amphora* shape, have arisen independently in a number of different phyletic lines, and that a classification on the basis of single or double rows of puncta, inner pores or no inner pores might be more natural. It might also help in dividing that monstrosity of a genus, *Navicula*.

F. HUSTEDT: *Gomphonema* und *Cymbella* unterscheiden sich nicht nur durch die Form

der Schalen, sondern besonders durch die Symmetrieverhältnisse der Zellen. Eine Mittelstellung nimmt die Gattung *Gomphocymbella* ein. Sie zeigt uns, dass die Natur keine scharfen Grenzen zieht; wir sind aber gezwungen, solche Grenzen anzunehmen, um ordnen zu können.

R. W. KOLBE (Stockholm)

On the Microstructure of Diatoms

An attempt is made to summarize the results of observations on Diatom shells since the introduction of the Electron Microscope. The electron micrographs demonstrated give examples of

1. the different types of "chambers" which correspond to the striae and puncta of the Diatoms as seen by the light microscope. The micrographs show also various details of the "sieve membranes" which seem to form an integral part of the chambers;

2. raphe. In several cases the raphe can be seen as an open slot, thus confirming the more or less theoretical view on this organ. An interesting special case is a kind of perforated girder combined with the raphe of some *Nitzschiae* (invisible by the light microscope);

3. details of mucous pores and processes (mostly tubes);

4. smooth homogeneous inner membranes; seta of *Corethron*;

5. cell wall of *Epithemia*—a structure for which there is no explanation yet.

Although it is too early to draw general conclusions out of the still scarce material, there is no doubt that the Electron Microscope shows new problems in Diatomology; it is a great help in some critical taxonomical problems (an example, *Stephanodiscus Binderanus*, is demonstrated), and it confirms in an impartial way most of the assumptions and observations made by the older authors by the light microscope.

Discussion

F. HUSTEDT: Besonders interessant ist die Aufnahme von *Nitzschia* sp., die den Bau der Raphe

erkennen lässt. Sie entspricht in ihrem Bau der Kanalaraphe bei *Epithemia* mit dem Unterschied, dass die Aussenwand mit dem Raphenspalz kielartig gehoben ist. So ergibt sich eine eindeutige Entwicklungsreihe von der *Navicula*-Raphe über die Kanalaraphe bei *Epithemia-Denticula* zur Gattung *Nitzschia* und schliesslich den Surirellen. — Die Deutung elektronenmikroskopischer Aufnahmen muss mit Vorsicht geschehen. Das Elektronen-Mikroskop ist nicht frei von Beugungserscheinungen, aber infolge der grossen Schärfentiefe sind etwaige Beugungsbilder nicht von den reellen Bildern zu trennen.

RUTH PATRICK (Philadelphia, Pa.)

Some New Methods for Dealing with Variation in Diatoms

This paper discusses two methods which have been developed in our laboratory for dealing with variation in diatoms at the inter- and intra-specific level.

The first method is a serological one. To the best of my knowledge this is the first time that serological methods have been applied to diatoms to see at what level it would be useful. Three genera of diatoms, *Navicula*, *Gomphonema*, and *Nitzschia*, were selected because taxonomically *Navicula* and *Gomphonema* are more closely related to each other than to *Nitzschia*. The species with which we worked were *Navicula pelliculosa*, *Gomphonema parvulum*, and three species of *Nitzschia*: *N. closterium*, *N. palea*, *N. linearis*. These species were chosen because *N. palea*, *N. linearis* are more closely related to each other than to *N. closterium*.

The diatoms were grown as single species in mass culture. The concentrate was centrifuged in a sonic centrifuge which broke open the diatom shells. This material was then filtered through a bacteriological filter which retained the shells and the bacteria. The nitrogen content of the clear filtrate was then determined so that a constant could be obtained if the experiment was to be reproduced. The ring test was used to determine the presence of a precipitate. The

only two sera which interacted at all were *Nitzschia palea* and *N. linearis*. This would indicate that diatom serum is very specific and will be useful in separating closely related species and taxa of the intra-specific level.

The second method for dealing with variation in diatoms is by the use of charts. Several characters are charted at once as set forth in "Introgressive Hybridization" by EDGAR ANDERSON. If these characters fall into definite groups you have recognizable units or taxa as defined by the characters plotted. However, if the characters plotted form a more or less continuous gradient, the variability of these characters is probably due to morphological variation in successive generations of the classes. This would indicate that the characters chosen are either not the correct ones with which to separate the taxa in question or that you have one widely varying taxon.

Discussion

R. Ross: Any attempt of plotting characters and trying to deduce by inspection the extent to which the points fall into groups is dangerous, if mathematical statistical tests of significance of the differences are not made.

RUTH PATRICK: I have often used statistical methods. It would be very difficult to describe mathematically the shape of the end of a diatom valve—and then treat the matter statistically. Varieties in diatoms are based in such perplexing questions on a group of characters. It would be very tedious statistically to correlate four such characters—and I doubt that it would show significant facts which are not observable by the manner of graphing.

LISELOTTE MOEWUS (Heidelberg)

Über einige Ursachen der morphologischen Variabilität bei der Gattung Enteromorpha

Infolge der starken morphologischen Variabilität bereitet die systematische Gliederung der Gattung *Enteromorpha* grosse Schwierigkeiten. Der Formenreichtum dürfte kaum auf

Bastardierung zurückzuführen sein. Unter konstanten Kulturbedingungen sollten sich bestimmte Merkmale konstant verhalten. Optimale Kulturbedingungen sind erst dann erreicht, wenn das Wachstumstempo in den Kulturen demjenigen an Standort während der günstigen Entwicklungsmonate entspricht. Es konnten innerhalb von 7 Monaten von den an der ostfriesischen Küste gesammelten Formen 3–8 Generationen aufgezogen werden. Die Entwicklung wurde mikroskopisch vom Festsetzen der Schwärmspore an über die Keimlingsstadien bis zur Schwärmerentleerung genauestens verfolgt. Trotz konstanter Kulturbedingungen wiesen die kultivierten Pflanzen keine morphologische Gleichförmigkeit auf. An 3 Kulturserien wird die Variabilität äusserer und innerer morphologischer Merkmale demonstriert (Thallus-Gestalt, Verzweigung, Anordnung und Grösse der Zellen, Stärke der Zellwand). Thalli, die aus abgetrennten Rhizoiden herangezogen wurden, hatten ein anderes Aussehen als die aus Zoosporen hervorgegangenen Pflanzen. In Reinkulturen von Rhizoid-Regeneraten, die von Pflanzen der 1., 2. oder 4. Generation angelegt waren, entwickelten sich unerwartet andere, niedere Algen. Es liess sich zeigen, dass diese nicht im Seewasser, das zur Kultur verwendet wurde, enthalten waren. Ihr Auftreten lässt sich dadurch erklären, dass sie in intrazellulärer Symbiose mit den *Enteromorphen* gelebt haben. Hinweise dafür sind 1. der monströse Bau der Rhizoide, 2. vergrösserte Zellen im Thallus, 3. Membranmissbildungen. Cytologische Untersuchungen ergaben, dass dem *Enteromorpha*-Kern ein kugeliges Gebilde angelagert ist, in dessen Mitte ein kleiner Kern erkennbar ist. Dieser symbiontische Körper scheint einen Einfluss auf den *Enteromorpha*-Kern auszuüben, indem er den normalen Generationswechsel stört. Alle 16 kultivierten Formen zeigten nämlich keinen Generationswechsel. Sie entleerten vielmehr ein Gemisch von 2- und 4-geissligen Schwärmern, oder über mehrere Generationen nur Zoosporen oder nur Gameten. Nur solche Gameten gelangten zur Entwicklung, die den symbiontischen Partner

bei der Schwärmerbildung mitbekommen hatten. In 4 Fällen konnten diese Symbionten in Reinkultur vermehrt werden. Es handelte sich um Vertreter der Heterokonten (*Pleurochloriella*, *Monallantus*) und um eine fädige Form, die sich nicht bestimmen liess. Intrazelluläre Symbiosen höherer Algen mit niederen Algen wurden bereits bei den Chaetophoraceen gefunden und beide Partner getrennt kultiviert.

Discussion

S. SUNESON: Ich fand den Nachweis sehr interessant, dass die *Enteromorpha*-Arten auch in Kultur unter ziemlich konstanten Bedingungen ihre äussere Form so stark verändern. Die Behauptung, aus einer haploiden Pflanze wäre eine Generation entstanden, in welcher ein und dieselbe Pflanze sowohl Gameten als auch Zoosporen erzeugt, ist sehr eigentümlich und sollte durch eine zytologische Untersuchung der Chromosomenzahlen nachgeprüft werden.

J. BRUNEL (Montreal)

Étude historique et phytogéographique de la phycologie canadienne

Cette étude comporte en premier lieu l'analyse de tous les travaux se rapportant à la flore phycologique du Canada: les dix provinces canadiennes, le territoire du Yukon, les districts de Mackenzie, de Keewatin et de Franklin, sont tour à tour passés en revue au double point de vue des Algues marines et des Algues d'eau douce.

En deuxième lieu, au point de vue de la distribution des Algues marines autour des côtes canadiennes l'auteur distingue cinq grandes régions: a) région colombienne; b) région arctique; c) région hudsonienne; d) région Baffin-Labrador; e) région laurentienne. Ces diverses régions sont ensuite subdivisées pour la plupart en plusieurs sous-régions.

En troisième lieu le territoire canadien est étudié au point de vue de la distribution des Algues d'eau douce, en fonction des grandes régions physiographiques déjà connues, dont les principales sont: montagnes Rocheuses,

prairies de l'Ouest, bouclier précambrien, Grands Lacs et plaine du Saint-Laurent, etc.

Pour conclure, l'auteur essaie de déterminer les caractéristiques essentielles de la flore d'Algues marines du Canada, et ses affinités asiatiques et européennes. Quant aux Algues d'eau douce, leur inventaire est encore trop peu avancé dans de vastes régions du territoire canadien pour qu'on puisse tirer des conclusions générales valides relatives aux associations qu'elles forment.

F. N. WOODWARD (Musselburgh)

Chemistry of the British Brown Marine Algae and Their Possible Industrial Utilization

The variation in chemical composition of the principal species of brown algae indigenous to Scotland has been determined on a monthly basis over a four year cycle. The chemistry of certain of the major organic constituents has also been studied, and methods are in course of development for their extraction on the commercial scale.

The industrial uses of the alginates will be reviewed and an indication will also be given of possible outlets for other algal chemicals.

The paper was read by Dr. F. T. WALKER.

Discussion

R. A. LEWIN: Have any intermediates—particularly phosphorylated hexoses—been isolated, which might be biological precursors of algin (polymannuonic acid)?

F. T. WALKER (Musselburgh)

Some Factors from the Sublittoral Seaweed Survey of Scotland

During the last four years we have been surveying the seaweed resources of the sublittoral zone around Scotland. The area of this zone down to 18 metres is approximately 500 000 hectares.

The Laminariae dominate the seaweeds of Scotland, both in size and quantity.

Stereoscopic aerial photography is employed for preliminary surveying. From such photographs the percentage of the substrate covered by seaweed growing over an area can be measured. There is some measure of coincidence between the depth at which the camera can record and the depth at which the brown seaweeds will grow abundantly, for both are photochemical processes. More than half of Scotland's 5 000 miles of coast has been subjected to preliminary surveying.

Should preliminary surveying indicate the presence of appreciable quantities of seaweed, then detailed surveying is carried out by methods which are essentially quadrat sampling of the seabed: a grab triggers on touching the seabed cutting off weed within a known area.

The species of plants, their fresh weight, depth at which they grew, and the time of the quadrat are recorded. Quadrats are taken at random or along measured transects, using buoys and a range-finder (WALKER 1947).

When the sampling data are plotted, taking only those quadrats which contained seaweed, the average fresh weight at various depths is very generally found to be greater as higher latitudes are reached.

On the other hand, when the sampling data are plotted to include all quadrats with and without seaweed and therefore bringing in the percentage cover, then where tidal streams are inappreciable, the weight is inversely proportional to the depth. In other areas where tidal streams occur, no such simple relationship holds. But in such areas it is found that the square root of the average fresh weight divided by the percentage seaweed cover is inversely proportional to the depth,

$$\frac{\sqrt{d}}{C} = k - \gamma f \text{ or } \sqrt{\frac{d_w}{C}} = k - \gamma f;$$

where d =average fresh weight of total quadrats at a particular depth, d_w =average fresh weight of quadrats containing seaweed at a particular depth, C =percentage seaweed cover at

the corresponding depth, f =interval of depth, and k & γ =constants for the area surveyed.

The slope of the graph is related to the extinction coefficient of light when passing through seawater, while the level of the graph is related to the rate of the tidal stream. The values for k at low water mark for twelve areas, ranging from N., S.W., and S.E. Scotland, and from which areas some 10 000 quadrats were taken, when plotted against the rate of tidal streams operating in the area during spring

tides show the plots all along two straight line graphs, one where *Laminaria Cloustonii* is the dominant alga and one where *Laminaria saccharina* is dominant.

Thus analyses of the surveys to date are resolving: 1. rate of tidal stream, 2. cover which is associated with the nature of the substrate, and 3. light absorption by seawater, as the principal ecological factors controlling the growth of the Laminariae, which algae dominate the sublittoral zone of Scotland, down to a depth of 12 metres.

SESSION 10

July 20th, 9 a. m.—1 p. m.

Chairmen: J. FELDMANN and F. E. FRITSCH, Recorder: J. A. NANNFELD

SUBJECT:

Bryophytes, Pteridophytes

K. MÜLLER (Freiburg i. B.)

Neue, für die Lebermoossystematik wichtige Merkmale

Gametophyten- und Sporophytenmerkmale gehen bei Lebermoosen nicht immer parallel. Dadurch entstehen für die Taxonomie und Phylogenie grosse Schwierigkeiten. Besonders zuverlässige Merkmale bei den einzelnen Arten und grösseren systematischen Einheiten sind deshalb sehr erwünscht. Das Sporogonstiel-Querschnittbild ist dafür schon längst bekannt.

Nach der Anheftung der Geiseln am Spermatozoid unterscheiden sich *Anthocerotales* und *Marchantiales* einerseits und *Jungermanniales* andererseits. Bei ersteren stehen beide Geiseln an der Spitze des Spermatozoids, bei letzteren sind sie im Abstand hintereinander befestigt. Darnach und nach zahlreichen anderen Merkmalen gehören die *Sphaerocarpaceae* zu den *Marchantiales* und die *Anthocerotales* können neben die *Marchantiales* gestellt werden. Die Stellung von *Monoclea* müsste daraufhin noch geprüft werden.

Die Zahl der Chromosomen im Gameto-

phyten gibt weitere Anhaltspunkte. Die Anthocerotales besitzen die geringste Zahl (5). Für die Artunterscheidung ist die Chromosomenzahl besonders wertvoll. Manche Arten sind diploid bis polyploid, z. B. *Pellia epiphylla* = 9, *P. borealis* = 18; *Riccardia pinguis*, *R. incurvata*, *R. palmata* = 10, *R. multifida* = 20, *R. sinuata* = 30 Chromosomen; *Cephalozia ambigua* = 9, *C. bicuspidata* = 18, *C. Lammeriana* = 27; *Nardia scalaris* = 9, *N. geoscypha* = 18, *N. insecta* = 36; *Chiloscyphus polyanthus* = 9, *Ch. pallescens* = 18. Die di- und polyploiden Arten zeigen grösseres Zellnetz und grössere Sporen usw. Es kann aber auch, allerdings selten, umgekehrt sein, z. B. *Solenostoma sphaerocarpaceum* hat kleineres Zellnetz und 18, *S. Levieri* grösseres Zellnetz und 9 Chromosomen.

Die Antheridien zeigen Unterschiede im Wandaufbau. Bei den *Cephaloziaceae* und *Hypogriella* liegen die Schmalseiten der Zellen alle auf einer Linie, die Wandzellen stehen also etagenförmig, bei den übrigen Jungermannien sind sie unregelmässig sechseckig. Abwechslungsreicher ist der Antheridienstiel, der aus

1, 2, selten 4 Zellreihen besteht und für viele Familien, Gattungen, besonders aber für die Arten charakteristisch ist. Auch die Zahl der Antheridien in den Blattachseln ist für viele Arten konstant.

Als besonders wichtiges Merkmal können die Ölkörper angesehen werden, die nur wenigen Gattungen oder Arten fehlen. Grösse, Zahl, Gestalt und Geruch sind für die einzelnen Arten typisch. So lassen sich z. B. schon an den Ölkörpern die *Harpanthaceae* von den *Lophocoleaceae*, das Subg. *Massula* von *Lophozia* und von *Leiocolea* unterscheiden; sie beweisen u. a., dass *Lophozia obtusa* nicht zu *Leiocolea* gehört. Schon an dem durch die Ölkörper bedingten Geruch lassen sich, neben anderen Merkmalen, *Targionia hypophylla* von *T. Lorbeeriana* unterscheiden.

Auch die Sporogonwand bietet nicht nur bei den Marchantiales und den thallosen Jungermannien, sondern auch bei den beblätterten Arten wichtige Unterschiede. Die Dicke schwankt bei diesen zwischen 9 μ bei *Cephalozia* bis 210 μ bei *Pleurozia* und die Schichtenzahl zwischen 2 und 7-8. Die Dicke der einzelnen Schichten und ihre Verdickungsleisten sind ebenfalls für die einzelnen Arten charakteristisch, so dass ein sehr abwechslungsreiches, systematisch wertvolles Bild entsteht.

Das Verhältnis Sporendicke zur Elaterendicke ist gattungsweise konstant, oder bei einzelnen Arten derselben Gattung verschieden, z. B. *Bazzania trilobata* mit dem Verhältnis 1:1, dagegen *B. triseriata* 3:1; *Lophocolea heterophylla* und *L. minor* 1:1, andere *Lophocolea*-Arten 2-3:1.

Discussion

H. BUCH: Ich möchte hier die Aufmerksamkeit auf noch zu untersuchende Chromosomenzahlen richten. ARNELL und ich haben aus Nord-Fennoskandien und aus Novaja Semlja von *Tritomaria quinqueidentata* und einigen *Lophozia*-Arten Pflänzchen gefunden, welche fast doppelt so grosse Zellen besitzen wie die gewöhnlichen südsandinavischen Formen dieser Arten. Zu untersuchen wäre, ob es sich

hier wirklich um Polyploidie handelt, wie zu erwarten ist. Wenn dem so ist, hätten wir unter den Lebermoosen die gleiche Erscheinung wie unter den Gefässpflanzen, d. h. eine grössere Neigung zur Polyploidie in alpinen und arktischen Verhältnissen als in temperierten.

MARGARET FULFORD (Cincinnati, Ohio)

Some Distribution Patterns of South American Leafy Hepaticae

The fossil record of Hepaticae, though meagre, indicates that the Anaerogynae had evolved to forms similar to some of the more advanced living genera in Upper Carboniferous times, and that the marchantiaceous and leafy forms were present in the Triassic. The sporophyte of the leafy *Naiadita* was as much specialized as are highly specialized living forms. This means that in addition to being old, at least certain lines of hepatics have changed very little in the long time from the Upper Carboniferous and the Triassic times to the present.

Hepaticae occupy microhabitats and microclimates which may be very different from the surrounding general habitat and climate, and therefore they may persist for a long time after the vegetation of which they were originally a part, has long since disappeared. It is reasonable, then, to suppose that the distribution patterns of the living Hepaticae may furnish more detailed evidence of the history of vegetation, past migration routes, past climate, and details of paleogeography, than do most of the higher plants.

The distribution of the leafy hepatics in South America includes the following types of genera:

1. Cosmopolitan and subcosmopolitan genera.
2. Endemics—26 genera of wide or local distribution occur in Tropical and South America only, and 14 of these are Lejeuneaceae. Of the world total of approximately 180 genera of leafy hepatics, 55 are endemics. These 55 endemic genera include the 26 genera of Tropical and South America, 2 North American, 4 Euro-Siberian and Mediterranean, 9 Sino-Japanese

(mostly local), 10 Malayan (mostly local), 3 African, and 1 from New Zealand. 3. Genera with discontinuous distribution: a) Bipolar (of several origins); b) in areas of the Southern Hemisphere—tropical genera (certain predominantly South American genera also occurring in Africa and reported from Sikkim); subtropical-temperate-Antarctic genera (more widespread in South America, the Antarctic Islands, New Zealand and Australia, Polynesia, the Malay Archipelago, Hawaii, and sometimes Africa, and many likewise occur in Sikkim); Antarctic genera (a small group occurring in S. South America, New Zealand, S. E. Australia, the Antarctic Islands, with some of the species circumpolar, and an outlier in Sikkim—in the genus *Lepidolaena* it is the same species).

The distribution patterns of these genera of South America and the Southern Hemisphere—tropical, temperate, and the Antarctic types—indicate that they were contemporaries at a time when free migration was possible between South America, Africa, Australia, New Zealand, and the Sikkim area in N. E. India. They also indicate that the Antarctic Continent without doubt has been of great importance in the distribution of genera and identical species in South America, the Antarctic Islands, Australia—New Zealand, and probably Africa. Another explanation must be sought to interpret the existing relationships between the flora of tropical America—Africa, or the temperate southern hemisphere, or the Antarctic, and Sikkim.

Since half the endemic genera of the world and most of the disjunct genera of the southern hemisphere occur in South America, this land mass is particularly significant in the studies of the evolution of the floras.

Discussion

SUZANNE JOVET-AST: Les cartes de répartition des Hépatiques projetées par Miss M. FULFORD font apparaître peu de relations entre les Hépatiques sudaméricaines et les Hépatiques africaines. Je pense que ceci est dû surtout à l'insuffisance des études concernant les Hépatiques

africaines. A ce point de vue les travaux de VANDEN BERGHEM nous réservent certainement des surprises. Déjà VANDEN BERGHEM a découvert en Afrique tropicale un genre de *Lejeuneaceae* *Holostipées* connu jusqu'alors seulement en Amérique du Sud.

H. PERSSON: As to *Lepicolea* I have also made a map of this genus and shall discuss it in my coming lecture.—As to the map of *Barbilophozia* the same very interesting distribution is to be found for *Ptilidium ciliare*. Previously only found in the northern hemisphere I have now got localities (not published) from both Patagonia and New Zealand.—As to *Telaranea nematodes* I have found it (unpublished) in collections from Tristan da Cunha just in accordance with the map by Dr. FULFORD.—As to *Lembidium* Prof. TH. HERZOG has worked out this genus (it is just being printed in *Svensk Bot. Tidskr.*) and showed that it consists of two different genera.

J. KUZYNIAK: How do collections in the southern hemisphere correspond in number with those made in the northern hemisphere?

H. PERSSON (Stockholm)

Some Problems Concerning the Bryophyte Flora of Alaska

1. Of the species found in Alaska some 85 % are to be found also in Europe (for pteridophytes and phanerogams the percentages are 66 % and 30 % respectively). When the bryophytes will have been studied as much as the vascular plants with regard to microspecies, the difference will greatly diminish.

2. Cultivation side by side of North American and European bryophytes as well as of bipolar species from both regions combined with cytological studies is proposed. Also, transposition of stones etc. with bryophytes down and up the mountains is proposed in order to see if critical forms are genotypically separated or not.

3. The occurrence in Alaska of the high-oceanic hepatic *Marsupella alpina* is notified, previously known from Europe only.

4. The pronounced sterility of the hyperoceanic bryophytes is generally supposed to be due to their high age. Another explanation is proposed: in a paper of 1939 on the moss flora of Madeira the author states that a low degree of fertility is characteristic of the oceanic genera. Therefore it is not surprising that the most hyperoceanic bryophytes are strikingly sterile.

In this connection attention is drawn to a lack in the bryological literature, namely, that so little attention is paid to the occurrence or absence of sporophytes. The fertility of a bryophyte is in many cases not pronounced in the region where the species is most abundant.

5. In a work on Macaronesian bryophytes the speaker states "an evident tendency . . . to form separate races . . . having longer, narrower . . . leaves" (contrasting to what has earlier been stated as to alpine-arctic regions). The same tendency seems to characterize the Pacific coast of North America.

6. In North America, especially in the West, some bryophytes are growing on other substrata than in Europe (each continent has generally its microspecies). Species occurring in Europe on rocks or earth are—always or often—growing on trees in North America. Different circumstances may play a rôle. It may be that once the same trees grew in Europe on which these bryophytes are now occurring in North America.

7. As to their age, conclusions may possibly be drawn from the substratum on which bryophytes are growing. Several groups generally supposed to be rather old, as *Andreaeales*, *Sphagnales*, most *Dicranaceae*, etc., consist of silicicolous species. Silicious localities have played a dominating part in the older times of the earth. On the other hand, many bryophytes, supposed to be younger, grow on trees or on calcareous substratum.

The 6 species of the moss genus *Hymenodon* (*Rhizogoniaceae*) are—judging from the literature—practically totally restricted to arboriform ferns. This, no doubt, gives full play to one's fancy.

Discussion

P. W. RICHARDS: Has Dr. PERSSON any information about the habitat of *Pleurozia* in Alaska? In Ireland the habitat is usually treeless moorland.

H. PERSSON: The habitat of *Pleurozia purpurea* in Alaska (3 loc. known) is in the literature given as "in very wet places." A specimen from Metlakatla grew, according to the label, "among mosses at base of trees". In the hyperoceanic region of Norway *Pleurozia purpurea* generally grows on wet or shady rocks.

J. KUCYNIK (Montreal)

The Occurrence of Grimmia teretinnervis *Limpr. in North America with Notes on its Distribution*

Over a half-century ago, K. G. LIMPRICHT described a strikingly characteristic species of *Grimmia* from Innervillgraten, Tirol, Austria: *G. teretinnervis*. Having only female plants in a relatively poor condition at hand, its author was unable to assign it to one of the various subgenera of *Grimmia*. The task of defining its true taxonomic position hinges upon the discovery of fruiting material, for in *Grimmia*, seta, columella, and calyptra are of paramount importance in establishing subgeneric or sectional status. The sporophyte still remains to be found.

The plant has been distributed in a number of important bryological exsiccata. Making its initial appearance in J. BREIDLER's "Kryptogamae exsiccatae", it appeared subsequently in those prepared by F. RENAULD and J. CARDOT, JOHN M. HOLZINGER, and, under as many as five different numbers, in BAUER's "Musci europ. et amer. exsiccati." Material distributed under the name, in MACOUN's "Canadian Mosses" belongs to two altogether different species of *Grimmia*.

Some of the characters which serve to distinguish *G. teretinnervis* are the presence of

hairtips on certain leaves while others on the same plant are mucous with a markedly obtuse apex. The small size of the leaf-cells, $7\ \mu$ to $9\ \mu$ in diameter, is another trait. However, the most distinguishing features are observed when examining leaf-sections, particularly those taken from the region between midleaf and the base of the upper third. Here the lamina, generally unistratose for several cells on either side of the costa, suddenly becomes uniformly bistratose or, occasionally, multistratose, if not variously uni-, bi-, and pluristratose. Strict attention must be paid to the structure of the costa: circular in section and convex on both surfaces of the leaf, it invariably shows two subtly delimited regions: an outer zone formed of a single row of larger cells encircles the central portion formed of slightly smaller and more compact cells.

The following distribution is compiled mainly from study of material obtained on loan from some of the more important herbaria. In the Old World, *G. teretinervis* seems confined to the Alps regions, central Europe: the Steiermark and Tirol provinces in Austria; the High Tatra region in Hungary; Bern, Grisons, Neuchâtel, Ticino, and Waadt Cantons in Switzerland. L. LOESKE (Die Laubmoose Europas, p. 54, 1913) lists a station in the Julian Alps, Italy. Of the four North American areas cited by G. N. JONES, Minnesota, Tennessee, Idaho, and Canada (apparently Ontario), the author has seen correctly determined material from the first-mentioned state only. He discusses the question of listing a station each for Kansas and Missouri from which he has seen two correctly determined specimens. He also reports a new record for the species in Percé, Gaspé County, Quebec, based upon the MARCEL RAYMOND collection No. 35 made there in 1948. The habitat of *G. teretinervis*, which seems to reside in some hidden combination of limestone and sandstone, finds a requisite substratum in the conglomerate of the Bonaventure formation which occurs in the area. Altitude does not appear to exert a controlling influence on the species' distribution as stations for it are known at levels ranging from 200 m to 1800 m.

E. B. COPELAND and Mrs. F. ASHLEY
GAUQUE (Berkeley, Calif.)

Life History of Ferns

This is a partial report on a decade's work by the junior author, assisted by the senior, on the germination of fern spores and the subsequent growths. Such work is not new; but use of air mail, and professional contact with pteridologists in many lands, have made it possible on a new scale. In spite of many failures, we have germinated the spores of more than 120 genera.

The results in most cases support the classification in the senior author's *Genera Filicum*. Thus, the young sporelings of *Polypodiaceae* (in the strictest sense, excluding *Grammitidaceae*) are remarkably uniform, however different the adult plants. The same is true of *Blechnaceae*.

Grammitidaceae have uniformly distinctive gametophytes, in many respects like those of *Hymenophyllaceae*. They constitute a sufficiently distinct family, as has been maintained by CHING and HOLTUM.

Prothallia are more diverse than has been appreciated, differing in rate of growth, in form, texture, color, posture, in rhizoids, glands and trichomes, in margins, in time and place of appearance of sexual organs; and all of these differences seem to be characteristic, sometimes of species, sometimes of genera, sometimes of larger groups.

The least uniform family, as judged by the gametophytes, is *Pteridaceae*, which may eventually have to be recognized as polyphyletic.

The least uniform genus is *Asplenium*, and the characters of the gametophyte may be useful in its dismemberment. Besides species without glands, there are others with at least five distinct types. One of these strongly suggests *Diellia*.

The occurrence of similar trichomes on the prothallia and on the stipes or whole fronds of the same species is a common phenomenon, and is of particular interest because of the involved problems of genetics.

We have observed apogamy in 40 species in

which it was previously unknown. In most cases, an apogamous species seems to be always so—to be “obligate-apogamous.” One may then question whether one has to deal with a species in the usual sense, or with a clone.

The paper was read by Dr. A. S. FOSTER.

Discussion

P. W. RICHARDS: The last slide showing transition from apogamous prothallus to sporophyte and back to gametophyte is exactly parallel to F. VON WETTSTEIN's results with diploid gametophytes of the moss *Phascum cuspidatum*.

R. E. G. PICHI-SERMOLLI (Firenze)

On the Nomenclature of Some Genera of Ferns

Notwithstanding the studies of several Pteridologists the nomenclature of some genera of ferns still remains unsettled. It is a fact that a single genus often receives two different names from authors, while some other names, used by almost all authors but illegitimate by the strict application of the International Rules of Botanical Nomenclature, are not included in the list of Nomina Generica Conservanda, and are therefore liable to be rejected and replaced by new names. In order to prevent this confused and harmful situation from being protracted further, it is necessary that the International Committee for the Nomenclature of Pteridophyta and Phanerogamae should settle the nomenclature of these genera of ferns. To facilitate this task the author has thought it advisable to undertake a revision of the nomenclature of the majority of the fern genera, and to propose the conservation of some of them whenever a name, although illegitimate, is in general use and not listed among the *genera conservanda*, or whenever the application of the Rules does not allow to establish the name for a genus unequivocally. The generic names needing conservation can be subdivided into the following eight groups:

1. Generic names currently accepted, which ought to be rejected as later homonyms. Since the earlier homonyms are regarded as synonyms, the conservation of the names in general use is proposed: *Angiopteris* HOFFM. (1796) vs. *Angiopteris* ADANS. (1763); *Gleichenia* SMITH (1793) vs. *Gleichenia* NECKER (1790).

2. Generic names universally adopted, which are illegitimate owing to the existence of older names for the same genus. The conservation of the more widely used name is advisable: *Schizaea* SMITH (1793) vs. *Lophidium* L. C. RICH. (1792).

3. Generic names unanimously adopted by all authors, which are orthographic variants of names previously published. Owing to their extensive use the conservation of the later names is proposed: *Danaea* SMITH (1793) vs. *Danaa* ALL. (1785).

4. Generic names which are validly published but which are antedated by names *haud recte condita* previously proposed, adopted by some authors. The conservation of the names validly published is necessary to avoid confusion: *Araiostegia* COPEL. (1927) vs. *Gymnogrammitis* GRIFF. (1849); *Coniogramme* FÉE (1852) vs. *Notogramme* PRESL. (? 1851); *Lastrea* BORY (1824) vs. *Thelypteris* SCHMIDEL (? 1762); *Matteuccia* TODARO (1866) vs. *Struthiopteris* HALL. (1768) and *Pteretis* RAF. (1818); *Platyserium* DESV. (1827) vs. *Alcicornium* GAUD. (1825).

5. Generic names which are adopted by some authors and rejected by others owing to the existence of older names which are not properly or uncertainly typified. The conservation of the more widely used names is proposed: *Cheilanthes* SW. (1806) vs. *Allosorus* BERNH. (1806); *Cryptogramma* R. BR. (1823) vs. *Allosorus* BERNH. (1806); *Drymoglossum* PRESL. (1836) vs. *Pteropsis* DESV. (1827); *Sphenomeris* MAXON (1913) vs. *Stenoloma* FÉE (1852).

6. Generic names, quite legitimate, which have been revived after a long time during which other names had been currently used. The conservation of the legitimate names may

be advisable: *Phyllitis* HILL (1756) vs. *Scolopendrium* ADANS. (1763).

7. Genera which have names universally adopted, but which have other names published in the same year, and for which the day and the month of publication is not yet established. In order to avoid possible changes if the date should be established, the conservation of the most frequently adopted names is proposed: *Anemia* SW. (1806) vs. *Ornithopteris* BERNH. (1806); *Lygodium* SW.

(1801) vs. *Ramondia* MIRBEL (1801), *Ugena* CAV. (1801), *Odontopteris* BERNH. (1801) and *Gisopteris* BERNH. (1801); *Pellaea* LINK (1841) vs. *Platyloma* J. SM. (1841); *Phlebodium* (R. BR.) J. SM. (1841) vs. *Chrysopteris* LINK (1841).

8. Genera which have two names published by the same author and in the same paper. Though later authors have not chosen the more correct name, the conservation of the one currently used may be advisable: *Pyrrosia* MIRBEL (1803) vs. *Candollea* MIRBEL (1803).

TAXONOMY: PHANEROGAMS, TPH

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Vice-Recorder: E. ASPLUND

SESSION 1

July 12th, 1—4 p. m., Attendance: 35 members

Chairman: H. J. LAM, *Recorder:* E. HULTÉN

SUBJECT:

System of Gramineae

H. J. LAM (Leyden)

Opening Remarks

The Organizing Committee of this Congress has thought fit to honour me by charging me with the chairmanship of this Session and in that function I take great pleasure to welcome you all.

It has been 15 years that we have not met, and since the Amsterdam Conference many things have happened both in our science and in our private lives. Therefore, before we resume our discussions, may I invite you to commemorate for a moment the numerous members of our Section and, in general, the numerous taxonomists of every description who fell victims of the last war. Will you please stand to your feet for a few moments while we think back to so many lamented friends and colleagues. — — — — Thank you.

I deem it appropriate at this first meeting of the Section for Taxonomy of Phanerogams, whose organization we owe to the untiring ef-

forts of Dr. HULTÉN, that we are the guests of the country which produced the greatest taxonomist of all times, CARL LINNAEUS. Many of us will make a pilgrimage to his homestead next Sunday and remember what a very remarkable man he was.

There has been a period, in the first quarter of the present century, when systematic science was no longer much estimated among botanists. Descriptive Botany was more and more replaced by Experimental Botany, notably Genetics and Physiology, and it seemed as though the mother science, as created and glorified by LINNAEUS, had lost its central position and was badly on the decline.

In our days, however, we may state with satisfaction that that black state of affairs has been overcome and that the science of Taxonomy is again full of vigorous life. Not only are we realizing that our task of descriptive botany has by no means ended, that numerous new taxa are waiting to be described and many old ones need a careful reconsideration, but Descrip-

tive Botany has gained an entirely different and new significance. It is no longer restricted to the conventional description of the dead remains of part of a life cycle but it strives at a detailed characterization of the life cycle in full, and herbarium work, though still the basic method in many groups, is to be seen nowadays against the background of Genetics, Cytology, Geography, Ecology, Experimental Morphology, Anatomy, Physiology and Phytochemistry, Paleobotany, Evolution, and Phylogeny. In fact, all these branches of botanical science have coalesced, and they are actually all auxiliary sciences to whatever field you have chosen for a special study to the benefit of our knowledge of life.

In this sense, Taxonomy is again a fundamental part of Biology and at the same time a focal one. Whether consciously or not, we are all contributing towards the ideal of our science, which may be expressed by the notion of Typology as I see it, i.e. a 3-dimensional, dynamic Typology. Through this modern development, Taxonomy has regained its appropriate place among the biological sciences and we are entitled to honour LINNAEUS without being laughed at by those who fail to understand his outstanding importance.

All the numerous branches of our science will be duly considered during the meetings of the days before us, either in separate or in joint sessions.

In expressing the hope that our discussions may be profitable both to Science and to ourselves, I declare the meetings of this section opened.

C. E. HUBBARD (Kew)
System of Gramineae

Manuscript not received.

R. PILGER (Berlin-Dahlem)
Bemerkungen zum System der Gramineae

Neuerdings sind mehrfach Versuche gemacht worden, das wesentlich morphologisch auf die

Struktur des Ährchens begründete System der Gramineen durch andere, besonders zytologische und anatomische Daten zu verbessern und vielleicht auch phylogenetisch zu unterbauen, wobei wichtige morphologische Daten offensichtlich vernachlässigt worden sind.

Demgegenüber ist zu betonen, dass zunächst die morphologische Betrachtung an erster Stelle stehen muss. Die Gramineen sind bei erreichter Organisationshöhe innerhalb der Monokotylen als Familie charakterisiert durch die Merkmale des Ährchens, der Typus der Familie ist in der Struktur des Ährchens begründet. Daher muss zunächst festgestellt werden, in welchen Gruppen der Typus des Ährchens am reinsten zum Ausdruck kommt, dass heisst, wie das Ährchen beschaffen sein muss, von dem aus durch Progressionen alle anderen abgeleitet werden können. Wie weit diese Progressionsreihen den phylogenetischen Linien entsprechen, ist bei der Breitenentwicklung der *Gramineae* ebenso wie in anderen Familien schwer zu sagen. Der Morphologe wird immer sogenannten phylogenetischen Systemen mit Misstrauen gegenüberstehen.

Suchen wir nach Formenkreisen, bei denen der Gramineen-Typus des Ährchens noch am reinsten zum Ausdruck kommt, so kommen wir auf *Pooideae* — *Festuceae* — *Festucinae* wie *Festuca* und *Poa* oder aber auf *Arundinaria*. Es sind zwei Hauptgruppen zu unterscheiden, in denen die Progressionen parallel verlaufen, einmal die *Bambusoideae*, und dann die Gesamtheit der anderen Gruppen. Bei den *Bambusoideae* liegen spezielle, dem Fortschritt bei den anderen Gruppen entgegengesetzte Entwicklungstendenzen vor, die schliesslich auch zur Auflösung des Ährchens führen, dessen Einheitlichkeit sonst bei allen Veränderungen festgehalten wird.

Bei der Bewertung der Merkmale der *Festucinae* sei erwähnt, dass die Mehrblütigkeit des Ährchens mit Minderung der Bildungskraft nach oben wohl ein primitives Merkmal ist, doch dass ihr allein keine grosse systematische Bedeutung beizulegen ist. In den verschiedensten Zweigen der Gramineen geht die Reduk-

tion im Ährchen bis zur Einblütigkeit, wobei die unterste Blüte erhalten bleibt. So ist die Tribus der *Agrostideae*, die bei den älteren Autoren (so noch bei BENTHAM) ganz heterogene Elemente umfassen, deren einziges gemeinsames Merkmal die Einblütigkeit des Ährchens ist, ganz aufzulösen.

Den *Festuceae* — *Festucinae* schliessen sich eine Reihe anderer Gruppen der *Festuceae* an, dann sind von ihnen die *Triticeae* und *Leptureae* abzuleiten.

Ein zweiter grosser Ast der *Pooideae* sind die *Aveneae* (zweifelhaft die *Danthoniinae*), von denen die *Arundineae*, *Arundinelleae* und *Phalarideae* sich ableiten. Die Gruppe der *Phragmitiformes* bei AVDULOV ist ganz willkürlich. Zahl und Form der Chromosomen können nur als Bestätigung morphologischer Daten von Wert sein und an sich keine Gruppen schaffen. Eine eigene Unterfamilie (*Eragrostoideae*) ist auf die *Eragrostae* (inkl. *Sporobolinae* und *Lycurinae*) und *Chlorideae* zu gründen; sie haben nichts mit den *Panicoideae* zu tun, zu denen PRAT sie rechnet; die Gruppe ist sehr fortgeschritten, auch in der Anatomie. Die dritte Unterfamilie sind die *Oryzoideae*, bei denen eine Deckspelze mit Blüte ohne Vorspelze und darüber eine leere Spelze entwickelt ist. Die *Panicoideae* endlich sind in ihrem alten Umfang zu erhalten. Eine Anzahl kleiner Gruppen ist zweifelhafter Stellung.

The paper was read by Dr. H. MELCHIOR.

J. R. SWALLEN (Washington, D. C.)
Grass Flora of Brazil

Manuscript not received.

A. MELDERIS (Uppsala)
Generic Problems within the Tribe Hordeae

The tribe *Hordeae* (*Triticeae*) is well separated from the other tribes of grasses by the combination of the following features: a compound spike, two glumes (sometimes strongly reduced), simple starch grains and rather large chromosomes of festucoid type in multiples of 7. On the other hand, the limits between the genera of this tribe

are in many cases not very sharp, due to the existence of transitional forms and a great number of natural hybrids. For this reason, most earlier authors accepted only some few large genera, e.g. KUNTH (1838), BENTHAM & HOOKER (1883), and ASCHERSON & GRAEBNER (1901), but, as they did not agree in the interpretation of these, many species were shifted back and forth from one genus to another. The first one to make cardinal changes in the classification of the *Hordeae* was NEVSKI (1933, 1936), who split the genera of *Agropyron*, *Elymus* and *Hordeum* and arranged these (small) genera into several natural groups. With the exception of the isolated *Brachypodiinae*, he distinguished in the *Hordeae* 3 series of genera, each with 2 subtribes: 1) *Clinelyminae* series: *Clinelyminae* and *Roegneriae*, 2) *Hordeinae* series: *Hordeinae* and *Aegilopiniae*, and 3) *Elyminae* series: *Elyminae* and *Agropyrinae*. In each series, one subtribe contains genera with spikelets in groups at each node of the rachis, the other subtribe genera with solitary spikelets; the latter genera, according to NEVSKI's views, are younger and have developed from the genera with spikelets in groups. Genera within one and the same series are more closely related to one another than to genera with the same type of spike within other series. The classification of NEVSKI has been accepted by PILGER (1947), except the splitting of *Agropyron* and the separation of *Aneurolepidium* from *Leymus* (*Elymus* sensu NEVSKI). The researches of STEBBINS et al. (1946, 1949) show that in cytogenetic behaviour the genera *Agropyron* and *Elymus* in the usual broad sense are not uniform. Thus, *Agropyron pauciflorum* and *A. Parishii* are more closely related to *Elymus glaucus* and *Sitanion jubatum* than to *A. Smithii* which, together with *Elymus condensatus*, *E. triticoides* and *E. cinereus*, forms another group of related plants. As regards GOULD's (1947) proposal to unite nearly all the North American species of the *Hordeae* into one genus, *Elymus*, it must be noted that he has neither shown sufficient grounds for uniting the genera nor defined the boundaries of his genus. The limita-

tion of such large complex genera will always cause great difficulties and any such proposal may easily lead to only one large genus, *Fruentum*, as proposed by KRAUSE (1903, 1913).

On the basis of his own morphological and genetical studies of the members of the tribe *Hordeae*, as well as on the cytogenetic evidence found in the literature, the author proposes the following modified system of the *Hordeae*: 1) subtribe *Roegneriae*: *Terrella* NEVSKI, *Roegneria* C. KOCH [incl. *Clinelymus* (GRIS.) NEVSKI], *Anthosachne* STEUD., *Sitanion* RAF., *Hystrix* MOENCH (= *Asperella* HUMB.), *Cockaynea* ZOTOV; 2) subtribe *Hordeinae*: *Hordeum* (JESSEN) HARZ (= *Cuviera* KOEL.), *Taeniatherum* NEVSKI, *Crithopsis* JAUB. & SPACH, *Psathyrostachys* NEVSKI, *Hordeum* L.; 3) subtribe *Agropyrinae*: *Elymus* L. (= *Leymus* HOCHST., incl. *Aneurolepidium* NEVSKI, *Malacurus* NEVSKI), *Elytrigia* DESV., *Agropyron* GAERTN., *Eremopyron* JAUB. & SPACH; 4) subtribe *Triticinae* (*Aegilopinae*), more closely related to the *Agropyrinae* than to the *Hordeinae*: *Haynaldia* SCHUR, *Secale* L., *Heteranthelium* HOCHST., *Amblyopyrum* EIG, *Aegilops* L., *Triticum* L. According to HUBBARD (1946), the genus *Henrardia* HUBBARD, based on *Lepturus persicus* BOISS., represents a separate (5th) subtribe *Henrardiinae*. As regards the genus *Brachypodium*, the author agrees with HYLANDER, who treats it as a separate tribe.

NILS HYLANDER (Uppsala)

Some Ideas Regarding the Systematics of Scandinavian Grasses

Working on a new Scandinavian flora, the author has found a systematical rearrangement of the grasses of this region to be necessary, since the system used by HOLMBERG in his Scandinavian flora (1922, 1926) has been outdated in many points by the recent investigations of, e.g., AVDULOV and PRAT. On the other hand, it seems impossible to follow the last-mentioned authors in dividing the grasses into two subfamilies, for rather many genera are \pm intermediate between the typical panicoid and

festucoid grasses. Therefore an arrangement in several tribes is proposed, as shown below. Genera represented only by introduced species are indicated in brackets.

Typical panicoid genera:

- I. *Maydeae*: [*Zea*]
- II. *Andropogoneae*: [*Sorghum*]
- III. *Zoisieae*: [*Tragus*]
- IV. *Panicaceae*: *Setaria*, [*Panicum*], [*Echinochloa*], *Digitaria*, [*Cenchrus*]
- V. *Eragrostideae*: [*Eragrostis*]
- VI. *Chlorideae*: [*Dactyloctenium*], [*Eleusine*], [*Cynodon*], [*Chloris*].

Intermediate groups:

- VII. *Spartineae*: [*Spartina*]
- VIII. *Danthonieae*: [*Sieglingia*]
- IX. *Molinieae*: *Molinia*
- X. *Arundineae*: *Phragmites*
- XI. *Stipeae*: *Stipa*
- XII. *Oryzeae*: *Leersia*
- XIII. *Nardeae*: *Nardus*
- XIV. *Glycerieae*: *Glyceria*, *Catabrosa* (?)
- XV. *Meliceae*: *Melica*.

Typical festucoid genera:

- XVI. *Festuceae*: *Festuca*, *Lolium*, *Vulpia*, [*Scleropoa*], *Poa*, *Puccinellia*, *Phippisia*, *Briza* (?), *Cynosurus*, *Dactylis*, *Sesleria* (?; perhaps a separate tribe).
- XVII. *Agrostideae* (*Aveneae*): *Koeleria*, [*Lophochloa*], *Trisetum*, *Arrhenatherum* (incl. *Helictotrichon*), *Avena*, [*Gaudinia*], *Deschampsia*, *Scolochloa*, *Arctophila*, *Aira*, *Corynephorus*, *Holcus*, [*Lagurus*], *Apera*, *Ammophila*, *Calamagrostis*, *Agrostis*, [*Polypogon*], [*Gastridium*], *Arctagrostis*.
- XVIII. *Phalarideae*: *Cinna*, *Alopecurus*, *Phleum*, [*Beckmannia*], *Phalaris*, *Hierochloë*, *Anthoxanthum*, *Milium* (?).

Affinities uncertain:

- XIX. *Monermeae*: *Parapholis*.

Festucoid grasses, triticiform group:

XX. *Bromeae*: *Bromus* s. coll.

XXI. *Brachypodieae*: *Brachypodium*, [*Trachynia*].

XXII. *Triticeae*: [*Secale*], [*Haynaldia*], [*Triticum*], [*Aegilops*], [*Eremopyrum*], [*Agropyron* (s. str.)], [*Elytrigia*], [*Elymus* (= *Leymus*)], [*Clinelymus*], [*Roegneria*], [*Hordeum*], [*Hordeum*].

From this survey, the genus *Coleanthus*, formerly found in Scandinavia, has been excluded; it forms its own tribe, *Coleanthae*, but its affinities are quite obscure. Also the relationship of *Monermeae* is still imperfectly known. *Brachypodieae* hold, in their floral features, an intermediate position between *Bromeae* and *Triticeae* but differ cytologically from both. *Bromeae* must, on chemical and other grounds, be separated from *Festuceae*. The latter group is, in accordance with HUBBARD's views, considered relatively primitive and placed next to *Glycerieae* and *Meliceae* but be-

fore *Agrostideae*. This tribe, in the wide sense of PILGER, i.e. including *Aveneae*, forms a very natural group to which also *Scolochloa* and *Arctophila* (placed by HOLMBERG near *Glyceria*) should be referred. On the other hand, *Alopecurus* and *Phleum* are removed to *Phalarideae*, as proposed by PILGER; here also *Beckmannia* and *Cinna*, with long-styled, apically protruding stigmas, seem to belong. *Milium* deviates in its mode of flowering but shows a strong resemblance with *Phalaris* in the texture of its lemma and may perhaps be placed here, too. *Molinia*, the only indigenous Scandinavian grass with purple stigmas (a typical panicoid feature), was provisionally placed by HUBBARD in *Danthonieae* but seems aberrant enough to form its own tribe, *Molinieae*.

Discussion

C. E. HUBBARD, TH. SØRENSEN, J. R. SWALEN and N. HYLANDER took part in the discussion.

SESSION 2

Jointly with Section PHC: July 14th, 9 a. m. — noon, See page 611

SESSION 3

Jointly with Sections CYT, EXT and GEN: July 14th, 2—5 p. m., See page 330

SESSION 4

July 17th, 9 a. m. — noon, Attendance: 37 members

Chairman: W. B. TURRILL, Recorder: E. HULTÉN

SUBJECT:

Natural System of Flowering Plants

V. VOUG (Zagreb)

Die Botanik im Systeme der biologischen Wissenschaften

I. Einleitung. Kurze Übersicht über die bisherigen Systeme der biologischen Wissenschaften.

ten. Die phänomenologischen Systeme von SPENCER, HAECKEL und HAACKE, die methodologischen Systeme von BURCKHARDT und BERTALANFFY, die logischen Systeme von DRIESCH, A. MEYER, TSCHULOK und UNGERER, und die biozoologischen Systeme von GAMS, DU

RIETZ und DOTTERWEICH. Die Mangelhaftigkeiten der bisherigen Systeme. Das Fehlen des Ganzheitsprinzips und der gegenseitigen Beziehungen der subordinierten Wissenschaften.

II. Die Darstellung des neuen dreidimensionalen Systems der biologischen Wissenschaften. Die Organismen betrachtet von der Kugeloberfläche. Die drei aufeinander senkrecht stehenden Achsen durchschneiden die Kugeloberfläche an Hauptbetrachtungspunkten, denen folgende Denkkategorien entsprechen: Sein und Werden, Aussen und Innen, Raum und Zeit. Diesen Kategorien entsprechen sechs logische Wissenschaftszweige nach dem Systeme von TSCHULOK: Morphologie und gegenüber Genetik, Physiologie und gegenüber Ökologie, Chorologie und gegenüber Chronologie. In Wirklichkeit gibt es keine Betrachtungspunkten sondern Felder der Betrachtung an der Kugeloberfläche. Von diesem Standpunkte ausgehend kann man folgende Wissenschaftszweige in der Biologie als Ganzheit unterscheiden:

1. Die organischen Wissenschaftszweige [Morphologie, Genetik, Physiologie, Ökologie, Chorologie und Chronologie]. Diese sind keine Teile der Biologie, sondern deren Organe ohne welche die Biologie als Ganzheit kaum denkbar ist.

2. Die synorganischen Wissenschaftszweige, welche zwei oder mehrere Betrachtungspunkte bzw. Felder als Ausgangsbetrachtung haben wie z. B. Phylogenie [Genetik & Chronologie], Entwicklungsmechanik [Genetik & Physiologie] oder Geobotanik [Morphologie & Ökologie & Chorologie] usw.

3. Die holomeren Wissenschaftszweige wie z. B. Zoologie, Botanik, Anthropologie oder Bakteriologie, Mykologie, Entomologie usw., welche vom Standpunkte der Ganzheit nur einzelne Gruppen von Organismen oder auch sogar nur Teile von Organismen untersuchen, wie z. B. Zytologie oder Histologie.

4. Die methodologischen Wissenschaftszweige, die nach Methoden der Forschung eingeteilt sind, wie z. B. komparative Anatomie, experimentelle Morphologie. Hierher gehört

auch die Systematik [Taxonomie], die das System als Methode der Forschung benützt.

III.¹ Die Botanik vom Standpunkte der Ganzheit besteht aus ihren Organwissenschaften: der Morphologie, Genetik [im weitesten Sinne], Physiologie, Ökologie, Chorologie und Chronologie. Alle anderen Wissenschaftszweige lassen sich in das oben gegebene Schema einfügen. Damit ist ein ganzheitliches System der botanischen Wissenschaft gewonnen. Eine solche Botanik, die nicht die Pflanze als morphologisches Objekt, sondern als lebendiges Wesen in Form von Pflanzen betrachtet, sollte wieder als Phytologie bezeichnet werden.

Discussion

W. ZIMMERMANN: Zwei Gesichtspunkte des Vortragenden sind besonders glücklich: 1) Wissenschaftszweige sind nur Betrachtungsweisen. 2) Ein- und zweidimensionale Beziehungen sind nicht ausreichend. Man fragt sich, ob ein wirklich natürliches Wissenschaftssystem nicht *multi-dimensional* ist, zum Beispiel: die Phylogenetik steht nicht nur zwischen Chronologie und Genetik, sondern es bestehen ebenso Beziehungen zur Morphologie, Ökologie, Entwicklungsphysiologie usw.

W. ROTHMALER: Phylogenie und moderne Systematik sind identisch. Die Merkmalsphylogenie nimmt den Raum zwischen Chronologie und Morphologie ein.

G. CUFODONTIS: Gerade im Zeitalter der Spezialisierung ist die ganzheitliche Betrachtung als synthetische Zusammenfassung der biologischen Wissenschaften von grösstem Wert. Ausserdem ist die Darstellung in Form einer Kugel nicht nur als Symbol dieser Ganzheit glücklich, sondern gewährt auch den Vorteil, alle Wissenschaften, nicht nur die existierenden, sondern auch diejenigen, welche noch nicht „geboren“ sind, räumlich in Beziehung zu allen anderen anzuordnen.

C. E. B. BREMEKAMP: Morphologie und Genetik scheinen doch nahe verwandte Wissenschaften zu sein und nicht Antipoden wie Professor VOUG es sich vorstellt, und dasselbe gilt auch

¹ Die Botanik als holomere Wissenschaft der Biologie.

für die Physiologie und die Ökologie. Die Chorologie und Chronologie gehören eigentlich gar nicht zu den biologischen Wissenschaften sondern zu anderen Wissenschaftsgebieten, die Chorologie zur Geographie, die Chronologie zur Stratigraphie, das heisst zur Geologie.

V. VOUK: Der Bemerkung, dass die Phylogenie sozusagen dasselbe wie Systematik ist, kann ich nicht beistimmen. Die Systematik ist eine reine Ordnungswissenschaft und als solche nur methodologisch. Die Phylogenie ist aber eine synorganische Wissenschaft, die eine ganz bestimmte Stellung hat und in dieser Stellung in Beziehung zu allen anderen organischen Wissenschaften steht.

Auf die Bemerkung von Herrn BREMEKAMP, dass Chorologie und Chronologie keine biologischen Wissenschaften sind, kann ich nur antworten, dass diese nur dann zur Geologie oder Geographie werden, wenn man Chorologie und Chronologie als Organe der Biologie betrachtet, und wenn man das ganze System der biologischen Wissenschaften ganzheitlich auffasst.

E. M. HERING: Die einzelnen Wissenschaften (z. B. Morphologie und Genetik) sind nicht Antipoden, der Hauptteil der Betrachtung ist darauf zu legen, dass beide die Achse gemeinsam haben, wodurch die nahe Beziehung ausgedrückt wird. Es gibt zwei Arten von Taxonomie: 1) die heutige, unvollkommene, und 2) die der Zukunft, die ideale. Man kann die erste in das Zentrum der Kugel stellen, aber die ideale Taxonomie wird sich aller Wissenschaften bedienen müssen, so dass sie das gesamte Volumen einnehmen wird.

F. MARKGRAF (München)

Morphologisch-phylogenetische Studien an Blüten der Rhoeadales

MURBECK hatte in einer sorgfältigen und weitblickenden Überschau alle Familien der *Rhoeadales* auf einen einheitlichen Typus zurückgeführt, indem er besonders das Andröceum untersuchte. Ein entscheidender Schritt dieser Vereinheitlichung ist der, dass die 4 Kronblätter

der Cruciferen als 2 gespaltene mediane erklärt werden müssen. Dann würde nämlich das Cruciferen-Diagramm z. B. mit dem von *Dicentra* gut übereinstimmen. Die medianen „Kronblätter“ von *Dicentra*, die im Dienst der Bestäubung besonders ausgestaltet sind, haben je 2 seitliche Lappchen oder Spitzchen unter dem Mittelteil; die entsprechenden von *Hypecoum*, die gleichfalls eine Bestäubungsaufgabe haben, wurden von MURBECK wegen der Antheren-Ähnlichkeit ihres Mittelteils nur mit einem Staubblatt verglichen. Aber wichtiger ist es in unserem Zusammenhang, ihre seitlichen Lappen zu beachten, die wie bei *Dicentra* unter dem Mittelteil (erheblich verzögert) entspringen, jedoch viel grösser sind und sich regellos decken wie die Kronblätter der Cruciferen. Es liegt nahe, diese ihnen homolog zu setzen mit Ausfall des Mittelteils. Von der anderen Seite her kann man nachweisen, dass bei *Sanguinaria* vollständige Kronblattsplattungen die Regel sind und dass diese sogar, wenn sie sich auf die Medianebene beschränken, genau den Cruciferentypus liefern, dazu mit schwacher Aus-sackung von 2 Kelchblättern. Einer solchen Deutung steht indes die Auffassung von EGGERS entgegen, dass die medianen Kelchblätter später entstünden als die lateralen. Die Untersuchung sehr vieler Cruciferenblüten führte mich jedoch zu dem Ergebnis, dass bei allen 2 laterale Kelchblätter ausgesackt sind, und dass die Medianebene der Blumenkrone einen zusammenfassenden Charakter hat wie bei *Dicentra* und *Hypecoum*; in ihr vollzieht sich die Zygomorphie (*Iberis*, *Teesdalea*, *Carponema*), gegen sie konvergieren die Ansätze der Kronblätter z. B. bei *Selenia aurea* und in der Jugend überhaupt, und in ihr ist auch die Knospen-deckung der Kronblätter stärker als in der lateralen. In diesem Sinne die Entwicklungsgeschichte nachzuprüfen, regte ich Frl. ALEXANDER an. Dabei entdeckten wir eine eigenartige Aufwölbung der Blütenachse der Cruciferen in der Medianebene, die bei den Papaveraceen fehlt. Frl. ALEXANDER lieferte nun folgenden Nachweis: die zuerst angelegten Sepala sind die medianen, die deshalb auch von

Anfang an decken und deckend bleiben. Sofort nach ihrer Anlage beginnt aber die mediane Hebung, die sie über die seitlichen emporbringt, woher sie dann auch eine höhere, daher spätere Leitbündelversorgung bekommen. Die Petala bleiben genau wie die Seitenlappen von *Hypocoum* auffallend lange auf dem Primordialstadium stehen. Auch die Art der Bündelversorgung (seitliche Kelchblattbündel aus den Kronblättern abgegeben) ist bei *Hypocoum* dieselbe. Diese seltsame Hebung erklärt nun zugleich auch, dass der erwünschte Übergangszustand des *Hypocoum*-Kronblattes mit reduzierten Mittelteil bei Cruciferen nicht existieren kann: durch die Hebung werden von Anfang an die Seitenlappen auseinandergedrängt. Wenn sie krankhafter Weise unterbleibt, kann im Mediansektor ein ungespaltenes Kronblatt auftreten.

Durch alle diese Beobachtungen ist erwiesen, dass die Cruciferenblüte der von *Dicentra* und *Hypocoum* wirklich echt homolog ist und dass MURBECKS Theorie zu Recht besteht. Demnach kommt den Hypocoiden (*Hypocoum* und *Sanguinaria*; *Pteridophyllum* ist auszuschliessen und eher an *Chelidonium* anzunähern) eine auffallende Ausgangsstellung innerhalb der *Rhoeadales* zu: von ihnen aus lassen sich die regulären und die dorsiventralen Fumarioideen ableiten und über *Eschscholzia*, deren Kronblätter sich nicht selten spalten, auch die Papaveroideen (mit Staubblattspaltungen). Von demselben Punkt gehen aber auch die Cruciferen aus und über *Cleome* die Capparidaceen (durch nachgewiesene Spaltung, MURBECK) und die Tovariaceen (mit vermehrten Gliedern in allen Blütenkreisen). Die Resedaceen zeigen an ihren Kronblättern Basalschuppen wie viele Cruciferen und Capparidaceen. Die Moringaceen und Bretschneideraceen klingen dagegen stärker an Leguminosen an als an Capparidaceen.

Bei der Frage, wo nun die Hypocoiden in entgegengesetzter Richtung angeschlossen werden können, stösst man auf *Podophyllum*, das in Laub und Blüte grosse Ähnlichkeit mit *Sanguinaria* hat. Die lateralen äusseren Perianth-

blätter sind schwach sackförmig, die inneren oft verdoppelt und bisweilen unvollständig gespalten. Somit werden auf diesem Weg die *Rhoeadales* an die Berberidaceen angeschlossen, deren Blüten sehr klar aus gekreuzten Quirlen aufgebaut sind, und damit an die *Ranales*.

Discussion

H. J. LAM: Ich möchte wissen, was „Spaltung“ ontogenetisch und phylogenetisch eigentlich ist. Glaubt der Vortragende, dass ein Organ, dessen Form z. B. auf einem genetischen Faktor beruht, sich je in mehrere gleichartige Organe spalten kann?

F. MARKGRAF: Eine ontogenetische Spaltung ist nicht beobachtet worden. Die „Tendenz“ zu (phylogenetischer) Spaltung ist in diesen Familien häufig. Ihre erbliche Grundlage könnte nur experimentell geprüft werden.

W. ZIMMERMANN: „Spaltung“ in phylogenetischem Sinn bedeutet, dass an Stelle weniger Ahnenorgane der Vegetationspunkt heute viele ausgliedert, z. B. bei *Ur-Rhoeadales* 6 Stamina, heute viele. Beweis hierfür scheint mir nicht erbracht. Ist bei der Cruciferenblüte „Hebung“ des medianen Sektors durch Messungen der Zellstreckung oder Zellteilung unmittelbar beobachtet? Ist es nicht denkbar, dass die später auftretenden lateralen Kelchblätter tiefer inseriert sind als die zuerst auftretenden medianen?

F. MARKGRAF: Messungen des Zellwachstums oder der Zellvermehrung sind nicht durchgeführt worden, können aber noch gemacht werden. Die Anlage der Sepala geht so vor sich, dass die lateralen unmittelbar nach den medianen entstehen und dann durch Wachstum des medianen Teils der Blütenachse über ihnen in der Tiefe zurückbleiben.

H. MELCHIOR: Ist in der Hebung des Torus bei den Cruciferen der Beginn des bei den Capparidaceen vorhandenen Gynophors zu sehen?

F. MARKGRAF: Mit dem Gynophor der Capparidaceen hat diese Hebung nichts zu tun, sie tritt schon auf der Höhe der Sepalen ein.

T. H. GOODSPEED and BROOKING TATUM
(Berkeley, Calif.)

*Demonstrations of Orthochromes Illustrating
the Flora of California*

Thirty photographic enlargements and fifty-five lantern slides, both in natural color, showed the elements and distribution of almost half of the twenty-eight plant communities recognized in the Californian flora by MUNZ and KECK (El Aliso, 2: 87-105, 1949; cf. *ibid.* 199-202). Of the eleven vegetation types which they list all but their strand, salt marsh, freshwater marsh and alpine fell fields were represented by valley grassland, foothill woodland, chaparral, sagebrush scrub, pinyon-juniper woodland, yellow pine forest, mixed evergreen forest, redwood forest, closed-cone pine forest and northern coastal scrub plant communities. The first five are part of the Upper Sonoran Life Zone and the remainder are part of the Transition Life Zone. Illustrations of members of the Coastal Strand, Canadian and Hudsonian Life Zones were also given.

The plant community concept is well suited to interpretation of a flora like that characteristic of California. With such diversity of site and climate as is provided by California's mountains and valleys, located as they are on a northwest coast, and with derivations from several diverse sources, a complex plant distribution is inevitable. While, like other systems foisted on nature by man, this system suffers from conventionalization, it comes closer to corresponding to the observed distribution of Californian plants than any scheme hitherto advanced.

The junior author, BROOKING TATUM (Burlingame, Calif.), who provided the photographs and slides, has for ten years been engaged in a photographic survey (in natural color) of the floras of the Pacific slope of North America, from Lower California to British Columbia. His work is done entirely in the field, of selected and typical plants *in situ*, in an effort to produce a permanent research record of the species of the various plant communities and of their immediate environment.

SESSION 5

July 17th, 1-5 p. m., Attendance: 30 members

Chairman: K. H. RECHINGER, Recorder: E. HULTÉN

SUBJECT:

Natural System of Flowering Plants

G. ERDTMAN (Stockholm)

Pollen Morphology and Plant Systematics

"Pollen grains very small, provided with three furrows" and "Pollen grains measuring about 25 μ " may serve as examples of summary descriptions of the pollen grains in certain plant families still to be seen in recent books on Systematics. Modern palynologists (Palynology: pollen and spore science) can, however, provide yet more exhaustive data. They do not only consider the apertures, shapes, and sizes of the

pollen grains but also—using a great number of special terms—the fine details of "sporoderm stratification" etc. as revealed by "Lo-analysis" and in other ways, electrone microscopy included. One of the paramount tasks of modern Pollen Morphology is to provide taxonomists with new additional data in contributions towards the elucidation of plant affinities.

In "eurypalynic" families Pollen Morphology often contributes to more detailed classifications; incidentally, this may also be possible in more or less stenopalynic families, such as

Cruciferae and *Labiatae*. In some genera, e.g. *Abelia* and *Morina*, the subdivisions (sections) are well defined also on the basis of Pollen Morphology, and it may be questioned whether some of the sections should rightly rank as genera or not.

In *Epacridaceae* the pollen tetrads are usually isodynamisporous (i.e., the four pollen grains have the same size); in *Leucopogon amplexifolia* and *L. australis*, however, they are anisodynamisporous, composed of one large and three more or less rudimentary grains. In these cases, and in many others, a development towards more "advanced" forms can be traced.

Some families, *Thurniaceae*, *Diclidanthraceae*, etc. should, on pollen-morphological and other evidence, be amalgamated with other families, whereas some withdrawn families had better be revived. The contribution of Pollen Morphology to the discussion on the affinities of *Butomaceae*, *Canellaceae*, *Casuarinaceae*, *Eucommiaceae*, *Euphorbiaceae*, *Pandanaceae*, *Thymelaaceae* and a number of other plants will be illustrated by lantern slides.

Discussion

H. MELCHIOR: Ich halte auf Grund eigener Untersuchungen die vorgetragenen Ansichten für besonders wertvoll für systematisch-phylogenetische Untersuchungen, doch halte ich es für nötig, dass auch die übrigen morphologischen Merkmale nicht ausser Acht gelassen werden, da sonst leicht falsche Rückschlüsse gezogen werden können (z.B. *Bignoniaceae*: Tetradenpollen in ganz verschiedenen Verwandtschaftsgruppen).

G. ERDTMAN: As to pollen morphology in *Gesneriaceae* and *Acanthaceae* too much importance should not be attached to the occurrence of tetrads. Some of the discrepancies between palynological and non-palynological characters may perhaps disappear if pollen morphology is studied along more modern lines than done by RADLKOFER and LINDAU.

H. J. LAM: I think that Dr. ERDTMAN has shown us that there is an enormous wealth of

information of great value for taxonomy, a new field which has been prolated by those of anatomy, phytochemistry, etc. Taxonomy or rather typology is badly in need of more facts and it owes Dr. ERDTMAN a great debt of gratitude.

H. J. LAM (Leyden)

Stachyosporry and Phyllosporry as Factors in the Natural System of the Cormophyta

Evolution and phylogeny are still largely matters of speculation. The methods of their investigation, beside Philosophy, are threefold: Paleontology, Cytogenetics and Taxonomy. The most promising method in the latter is the typological one. This was established as a purely static method, but phylogeneticists hold that it must be possible to combine typology of recent organisms with the data offered by paleontology as traces of developments along the time axis. Thus, a phylogenetic-typological system is strived at, which is to replace the ancient so-called phyto-genetical systems which were mostly based, not on paleontological evidence, but merely on supposed relationships (similarities) of living organisms.

In such a system the "vertical trends" (i.e. those along the time axis) will be the most prominent feature. They are chiefly based on a typological combination of character phylogenies in the sense of W. ZIMMERMANN, as far as compatible with the logics of cytogenetics. A logical adjustment of these lines to the typological system of living organisms should be attempted.

In this connection the author has tried to test the value of stachyosporry (sporangia axis-borne) and phyllosporry (sporangia leaf-borne) as conceived by him in 1948 on the basis of SAHN's *Stachyospermae* and *Phyllosperrae*, both for practical classification purposes and for deepening our insight in the intrinsic structure of the *Cormophyta*.

It is pointed out that, while most lower *Cormophyta* (*Psilopsida*, *Lycopsida*, *Sphenopsida*) are stachyosporous and only the *Filicales* are fully phyllosporous, some of the higher

groups, probably in this respect on the basis of the more or less mixed *Pteridospermae*, are of an intermediate nature. It is true that *Ginkgo*, the *Chlamydospermae* and probably *Casuarina* may be considered fully stachyosporous and the *Cycadales* phyllosporous, but the *Benettitales* and most of the *Coniferales* (and possibly the *Cordaitales*) are stachyosporous in the female, and, in various degrees, phyllosporous in the male organs.

In the angiosperms the conditions are more complicated; moreover, the majority has not yet been sufficiently investigated from this point of view.

It is suggested that the distinction in *Stachysporae* and *Phyllospora* is older than that in *Monocotyledones* and *Dicotyledones*. The former is based primarily on the insertion of the ovula; but relationship and, occasionally, the shape and position of the stamens (e.g. epipetalous prevails in stachyosporous groups), as well as traces of ancient dichotomies both in filaments and funiculi and in venation, add quite some substantial support. However, in general the stamens yield less evidence than do the ovules, but it is believed that their alleged uniformity is less strict than is usually asserted.

All this would mean that the angiosperms, in spite of their high common specialization (embryology), are to some extent at least biphyletic, a supposition which is not contradicted by the more trustworthy data of paleobotany. The ancestral stock is believed to be pteridospermous, possibly somewhere near the *Caytoniales*.

It is provisionally concluded that the *Stachysporae* comprise: the *Monochlamydeae* (to be subdivided into a more or less heterogenous woody group and a more homogenous herbaceous group: *Polygonales*, *Centrospermae* with the sympetalous *Plumbaginales*, *Primulales* and probably *Convolvulales* and *Ebenales*), and of the *Monocotyledones* the *Helobiae*, *Spadiiflorae* and *Pandanales*. Particularly among the *Helobiae* (of which *Najas* is considered the most primitive representative) relationships with the herbaceous *Monochlamydeae* are pointed out. Possibly stachyosporous are also the *Malvales*,

Geraniales, *Celastrales*, *Rhamnales*, *Myrtales*, *Oleales* and *Plantaginales*.

The *Phyllospora* first of all consist of the *Polycarpicae* and derivatives (*Rhoeadales*, *Rosales*, *Guttiferales*, *Contortae* and *Tubiflorae*) and among the *Monocotyledones* of the *Liliiflorae* and all other orders not mentioned under *Stachysporae*. Possibly phyllosporous are also the *Parietales*, *Rubiales*, *Cucurbitales* and *Campamilales* (*Symandrae*) and perhaps also *Proteaales*, *Santalales* and *Hamamelidales*.

Much detailed investigation, however, will be needed to check the value of these suggestions and to find out whether the two types are actually recognizable among these doubtful and the still unmentioned orders or whether stachyosporous and phyllosporous are so much mixed up there that no clear distinction is possible. Even so, however, the two notions are believed to be of fundamental significance for the natural system of the *Cormophyta*.

A full account of this lecture is printed in *Svensk Botanisk Tidskrift* 44 (1950) pp. 517-534.

Discussion

K. FAERGRI: How does the concept of *Euphorbiaceae* as a primitive family fit into the picture of stachyosporous and phyllosporous respectively?

H. J. LAM: To my mind the *Euphorbiaceae* is really one family, thus a very much displaced one. It is undoubtedly stachyosporous, but whether it is primitive can only be stated on the strength of paleobotanical evidence.

V. PURI: The conception of stachyosporous and phyllosporous seems to be based on one character only, the position of the ovules on "stem" or "leaf". This distinction fades into insignificance in the light of the telome theory to which Dr. LAM subscribes. My other objection deals with details which cannot be discussed at this moment.

W. ZIMMERMANN: Der vom Verfasser vertretene Grundgedanke: keine "Alluvialphylogenetik" sondern eine echte historisch ausge-

richtete Phylogenetik zu betreiben, ist unbedingt zu begrüßen. Es scheint aber gerade aus diesem Grunde bedenklich, ein einziges Merkmal in den Vordergrund für die taxonomische Gruppierung zu stellen. Sicher ist der Gegensatz der stachyosporen und der phyllosporen Plazentierung beachtenswert. Meines Erachtens ist bei Angiospermen Stachyosporie vielfach parallel entstanden.

Andere Deutungen scheinen z. B. für *Caryophyllaceae* (offensichtlich reduzierte Scheidewände bei *Tunica*, *Silene*, *Cucubalus*) schwer vertretbar.

H. J. LAM: I am not going to enter into details. The whole thing, as far as the angiosperms are concerned, is still very immature.

C. E. B. BREMEKAMP: It seems to me that the foundation on which the distinction stachyosporous or phyllosporous forms in the group of the *Cormophyta* has been based, rests on the assumption that the parts, which in the plants are commonly indicated as stem and leaves, are fully homologous, a view against which very serious objections may be raised. With regard to the possibility of distinguishing in the Angiosperms a phyllosporous and a stachyosporous group, it would perhaps be better to postpone a decision until it has been proved without the least doubt that the insertion of the ovules and the structure of the stamens cannot everywhere be interpreted in the same way.

H. J. LAM: I am not defending the scheme. I have thought about it, and perhaps I am wrong, perhaps I am right. Everybody is perfectly free to take it or to leave it, but in "leaving" it a counter-argument might be expected.

B. P. G. HOCHREUTNER (Genève) *Réflexions sur la taxonomie des Malvacées*

Nous avons déjà exposé (in *Bull. du Museum de Paris* 1949, p. 733-36) les raisons qui nous font considérer les Malvacées comme une famille distincte des Tiliacées, Sterculiacées et même des Bombacacées.

En revanche, la taxonomie de la famille pour-

rait être modifiée avec avantage. Elle est basée avec raison sur la structure des fruits.

Ceux-ci présentent le maximum d'uniformité chez les *Hibisceae* où il constituent une capsule de structure classique.

Au contraire, les *Malveae* ont des fruits d'une complication souvent très grande, comme nous l'avons décrit chez de nombreux genres (voir nos notes in *Annuaire du Conserv. et Jard. bot. Genève*: VI, 11-12, t. I, 1902; IX, 184-188, t. I, 1905; XV-XVI, 297-303, t. I, 1913; XX, 29-68, 1916; XXI, 347-387, 31 fig., 1920). Il faut donc les considérer comme une seconde tribu à évolution plus avancée.

Enfin, les *Urenaee* avec leurs 5 carpelles et leurs 10 styles, très constants, présentent incontestablement l'évolution la plus poussée et peuvent être considérés comme la dernière tribu et la plus évoluée de la famille.

H. HUMBERT (Paris)

Une merveille de la nature à Madagascar

Première exploration botanique du massif de Marojejy (N. E.). Future Reserve Naturelle integrale.

L. BENSON (Claremont, Calif.)

Relationships of the Ranunculi of the Continental Divide and of the Pacific and Eastern Forests of North America

In North America the species and varieties of *Ranunculus* occurring in the arctic regions, the alpine areas of the western mountains, the Rocky Mountain forests, and Sierra Madre Occidental of northwestern Mexico are related but different, since they are nearly all members of the section *Epirotes*. This relationship is summarized in the table below.

The species of the section *Epirotes* are confined to boreal regions and essentially to a North-South band along the Continental Divide from Canada into Mexico, and the group is almost unknown elsewhere on the continent. Although the forests and woodlands of the Pacific Region and of the Atlantic area apparently are

	Significant species ¹	Total species ¹ of <i>Epirotes</i>	American endemic species ¹	Endemic species ¹ of <i>Epirotes</i>
Arctic	10	8	4	4
Western Alpine	14	13	12	12
Rocky Mountain Forests..	18	13	11	8
Sierra Madre Occidental..	12	7	9	7
Totals	54	41	36	31

¹ In all cases species and geographical varieties.

favorable ecologically for *Epirotes*, it is not represented (at least typically) in either place, as shown by the following table:

	Significant species ¹	Total species ¹ of <i>Epirotes</i> ²	American endemic species ¹	Endemic species ¹ of <i>Epirotes</i>
Boreal, Alpine, Rocky Mt. For., and Sierra Madre Occidental	54	41	36	31
Pacific Northwest	33	0	25	0
Pacific Southwest	17	0	10	0
Eastern Forests	21	6	20	5

¹ In all cases species and geographical varieties.

² Aberrant species within the section.

The species of *Ranunculus* occurring in the Pacific Northwest, the Pacific Southwest, and the Eastern Forest floras of North America are endemic members of other groups than *Epirotes*. These species groups are related to others occurring in miscellaneous areas outside North America. There is no comparably close connection to the species of any one special region as with Continental Divide species, and relationships to Old World types are more remote. As shown by many plant groups, including the *Gymnospermae* and the *Pteridophyta*, the Pacific and the Atlantic floras are highly endemic, not showing the close connection with the boreal and sub-boreal floras of the Northern Hemisphere to be found along the Continental Divide.

The contrast in relationships of the species occurring in the ecologically more or less similar forests of the Rocky Mountain States and those

of the Pacific States is particularly striking. On ecological grounds these forests have been divided primarily according to altitude rather than mountain range, but in floristic composition they differ primarily according to mountain range as indicated by *Ranunculus*.

A. LOURTEIG (Tucumán)

Ranunculaceae of Temperate South America

This paper is a study of the species of *Ranunculaceae* occurring in Argentina, Chile and Uruguay, and also of those of southern Bolivia, Paraguay and Brazil, which are common to both groups of countries.

Eight genera are found in Argentina. This is the richest country in genera and species, especially in the southern zone. The next richest is Chile, which lacks the tropical genera *Clematis* and *Thalictrum*, which, coming from Brazil and the northwest of South America, reach Uruguay and the centre of Argentina.

The work has been undertaken from the systematic point of view, and gives generic descriptions covering the species studied and practical keys for the determinations of the species.

Anemone, *Barneoudia*, *Callia*, *Clematis*, *Hamadryas*, *Myosurus*, *Ranunculus* and *Thalictrum* with a total of 57 species and 10 varieties and forms have been studied. The geographical distribution of each is given and the species are described with citations of almost all the material which has been revised. Although abundant material has been studied from other countries, it is not mentioned unless a type or a topotype is concerned.

All the species have been illustrated with drawings, which so far as possible show the habit of the plant and dissections of the floral organs and carpels, the necessary elements for the determination and identification of species. Phototypes are included.

The work concludes with an alphabetical index of the genera and the valid species, as well as of the synonyms and the literature.

One new species is described for Argentina, *Ranunculus Hillii*, one new name is created,

Ranunculus Dusenii; and the following combinations are made: *Ranunculus bonariensis* var. *phyteumifolius* (St. Hil.), *R. bonariensis* var. *triseptus* (GILL, ex HOOK. & ARN.), *R. Cymbalaria* f. *exilis* (PHIL.), *R. uniflorus* f. *bolivianus* (PHIL.), *R. praemorsus* var. *sibbaldioides*, and *Hamadryas magellanica* var. *paniculata* (HOOK. f.).

Many names cited for the floras of these countries have been reduced into synonyms.

On the other hand, *Clematis dioica* var. *australis*, *Ranunculus trichophyllus*, *R. uniflorus*, *R. praemorsus* and *R. acaulis* are cited for the first time for Argentina.

Discussion

H. J. LAM, L. BENSON, W. B. TURRILL and E. HULTÉN took part in the discussion.

SESSION 6

July 18th, 9 a. m. — noon, Attendance: 28 members

Chairman: R. C. ROLLINS, Recorder: E. HULTÉN

SUBJECT:

Various Papers

K. H. RECHINGER (Wien)

Flora and Vegetation of Iran

The author is engaged in the preparation of a flora of the Iranian highlands, comprising Persia, Afghanistan, Baluchistan and the bordering mountainous districts. He has travelled twice through Persia. The following division in phytogeographic entities is a tentative one and is limited to the western part of Iran occupied by the Persian Empire.

1. *Central Iranian district* comprising also the mountain ranges of the inland and the inner sides of the bordering mountain ranges. This territory forms the Iranian part of the Irano-Turanian region.

Climate features: Few precipitations, long-lasting period of drought, important daily and annual fluctuations of temperature, severe winters, lower minima of temperature than would be expected on this latitude, two rest-periods.

Features of flora and vegetation: Woods and highgrown bushes lacking or scarcely represented. Great richness in species. Many endemic genera and species. Enormous richness of species in some genera, viz. *Astragalus* 700 spec., *Cousinia* 250 spec., *Nepeta* 150 spec.,

many *Chenopodiaceae*, *Compositae*, *Labiatae*. Many species occupy only small areas. Many dwarf- and halfshrubs, annuals and bulbous plants, comparatively few grasses. Many low bushes are very spiny and characterize an intermediate altitudinal zone of mountain vegetation. Nival belt not rich in species, rather few endemics, most of the high mountain species related to Irano-Turanian groups.

2. *Kurdic-SW Iranian district* separating the Iranian highland and the Mesopotamic lowland part of the Irano-Turanian region, forming the direct continuation of the utmost ranges of southern Taurus in the NW, going to East as far as Bushir-Shiraz.

Climate features: Not exactly known to me but evidently more moisture of air and less fluctuations of temperature in intermediate altitude zones, perhaps even more precipitations.

Features of flora and vegetation: Xerophilous, loose woods of *Quercus Brantii* and *Acer cinerascens* accompanied by *Amygdalus*, *Crataegus*, *Rhamnus* etc. Undergrowth rich in species, many endemics. Very important Mediterranean irradiations, viz. many annual *Trifolia* and *Medicagines*, *Populus euphratica* and *Salix*

acmophylla accompanied by *Vitex*, *Nerium*, *Ficus*, *Myrtus* and *Tamarix* penetrating far inland through the gorges of streams. *Vitis persica* as liana. Altitudinal zonation apparently clear but not studied by me. Belt of erinaceous shrubs and nival belt represented, both rich in endemics, most of species of mountain belts having Irano-Turanian relations.

3. *Southern Iranian district*. Comprising the southernmost part of Persia, east of the line Bushir-Shiraz, the former British Baluchistan and southern parts of Afghanistan. Even its western Persian part still incompletely known.

Climate features: High dryness of air (coastal districts excepted), large temperature, minima in the lowlands never, in the mountains rarely, below zero. Important daily fluctuations of temperature, few and irregular precipitations during the winter. Rest-period of vegetation none or very short, in lowland in summer, in highland in winter.

Features of flora and vegetation: Saharo-Sindian species are dominating. Flora not rich in species especially when compared with the Irano-Turanian and the Mediterranean region, often not rich in individuals, nearly no family peculiar to this region, no genus rich in species, species occupying large areas predominant. All these features known as characterizing the Saharo-Sindian region in general, might even be observed in the southern Iranian district but as this comprises mainly mountains, uniformity of flora and vegetation is less pronounced than in the Arabian and African parts of Saharo-Sindian region. Some important endemics occur in the mountains, each one forming a special community of plants, viz. the dwarf palm, *Nannorrhops Ritchiana*, and the spiny shrub *Stocksia brahuica* (*Sapindaceae*) and *Cousinia Stocksi*, though belonging to an Irano-Turanian genus, limited to the Saharo-Sindian mountain districts of Iran. Loose communities of *Acacia* recalling savannahs. *Euphorbia larica*, an endemic with succulent leafless stems, covers rocky slopes. More grasses occur than in the Irano-Turanian region, especially *Andropogoneae* and *Panicaceae*.

4. *Hyrcanic district*. Comprising the lowlands on the southern coast of the Caspian Sea and the northern slopes of Elburs-range from Araxes in the West till westernmost Khorasan in the East.

Climate features: Temperature only exceptionally below zero. Unimportant daily and annual fluctuations of temperature. Great and fairly constant moisture of air, precipitations all over the year in lower level. Moisture of air and precipitation diminishing from West to East and from sea-level to the mountain-belt. A layer of clouds on about 2500 m corresponds to the upper limit of forest.

Features of flora and vegetation: Forest of deciduous trees dominates: up to 1000 m *Parrotia persica*, *Pterocarya fraxinifolia*, *Albizia Julibrissin*, *Acer insigne*, *Acer laetum*, *Diospyros lotus*, *Gleditschia caspica*, *Zelkova crenata*; from 1000 to 2500 m: *Quercus macranthera*, *Q. castaneifolia* and *Fagus orientalis*. Many shrubs as *Crataegus*, *Prunus*, *Pirus*, *Malus* etc. Lianas as *Hedera*, *Vitis silvestris*, *Periploca graeca*, *Smilax* and *Tamus*. *Albizia*, *Parrotia*, *Gleditschia* and *Quercus castaneifolia* are endemic. *Pterocarya*, *Acer laetum*, *Diospyros* and *Zelkova* occur even in the Kolchic forests of Trans-Caucasia and N. E. Anatolia, *Pinus*, *Picea* and *Abies* as well as *Rhododendron* represented in both Caucasus and Anatolia and Hindukush and Himalaya are completely lacking in Iran. Rich herbaceous undergrowths with Euro-Siberian, Mediterranean and endemic components. On locally dry slopes forests of *Cupressus sempervirens* var. *horizontalis*. Between 2500 and 3200 (–3500) m a belt of low erinaceous shrubs composed of Irano-Turanian species. Rivers accompanied by high herbaceous perennials. Nival belt not rich in species and individuals but rather rich in endemics, very poor in Arcto-Alpine elements.

Discussion

H. MELCHIOR: Das Elburs-Gebirge war eine wichtige Wanderungsstrasse von Central-Asien nach Europa. Existierte früher ein zusammenhängender *Juniperus procera* - Wald im Elburs-Gebirge?

W. B. TURRILL: I wish to express my thanks to Dr. RECHINGER for his masterly summary of the rich flora and vegetation of Iran and also for his other extensive studies in the Nearer East. It may be of interest to recall that the first plate published on Febr. 1, 1787, in the Botanical Magazine was one of *Iris persica*.

A. C. SMITH (Washington, D. C.)
The Vegetation and Flora of Fiji

Vegetational types in Fiji are controlled by two principal factors, rainfall and type of soil. On the larger islands the basic rocks are mostly plutonic, but many of the smaller islands, such as those of the Lau Group, are upraised limestone. The limestone soils of Lau support a very dense forest of varied elements, whereas the volcanic soils of that region are marked by a comparatively poor flora. On the larger islands the southeastern slopes receive a heavy rainfall (often more than 200 inches annually) and support a dense rain-forest. The northern and western slopes have a lighter rainfall (usually 70–80 inches annually) which is markedly seasonal, with six comparatively dry months; on these slopes the predominant vegetation-type is grassland, with scattered thickets and pockets of forest. Transitions between the grassland and forest are usually fairly abrupt. Conditions of exposure on the higher mountain-ridges affect the aspect of the vegetation, but in general rain-forest ascends to the summits (highest elevation 1323 meters). Variations in temperature throughout Fiji are comparatively slight.

The flora is as yet inadequately known. Of the 1782 species of phanerogams thus far recorded from Fiji, 529 (29.7 %) are adventive. Of the 1253 known indigenous species, nearly 70 % are endemic. An analysis of the indigenous non-endemic species shows that nearly the half are pantropical or pan-Pacific. Of the endemic species, 784 (more than 90 %) have their closest relationships in the floras of Malaysia or Papuasia, indicating that most of the floristic elements of Fiji entered the region through the New Guinean—Melanesian route. About 5 % of the endemic species have close relationships

with New Caledonian or Australian plants, while a smaller number indicate the presence of Polynesian, New Zealand, or "Antarctic" elements in the Fijian flora.

An analysis of the 444 genera represented by indigenous species of phanerogams shows that about 33 % occur in both hemispheres, while more than 50 % are Indo-Malaysian. Elements derived from the New Caledonian, Australian, and Polynesian floras are comparatively small. Only thirteen genera are thought to be endemic, contrasting strongly with the large number of endemic species. There is one endemic family, *Degeneriaceae*.

A paper on the same subject is published in the Scientific Monthly LXXIII (1951).

F. R. FOSBERG (Washington, D. C.)
The American Element in the Hawaiian Flora

When tabulated on the basis of the probable original successful immigrants, about 18 % of the seed plants and 12 % of the ferns in the Hawaiian flora are of American origin. Of a total of 272 probable original successful colonizations by seed plants, about 50 are regarded as of probable American origin, while of 135 original colonizations by pteridophytes, about 16 were probably American. Calculating the percentages in this way, rather than on the basis of the total of about 1900 species and varieties now recognized in the indigenous Hawaiian flora, a significantly higher, and probably truer, proportion of the plant immigration came from America than has commonly been thought.

The interesting thing about this American element is the closeness of many of its members to their American kin. Fully half of the plants of American origin are either identical with, or only varietally distinct from American species. This may probably indicate that they have not been isolated from their American relatives for a very long time, in other words, that they are to be considered recent immigrants.

This fairly well shows that there have, even in geologically recent time, been available open habitats for colonization in the Hawaiian Is-

lands, that transoceanic migration across at least 2500 miles without stepping-stones is not only a possibility but a relatively common occurrence, and that one does not have to resort to past land connections to account for the flora of an oceanic island. It is presumed that none of the bridges that have been suggested to connect the Hawaiian Islands with other regions are considered to have been as recent as these colonizations from America.

F. VERDOORN (Waltham, Mass.)
Some Problems of Botanical Historiography

An introductory discussion of the relations between Cultural History and Natural History

is followed by a plea for more individual, as well as for more cooperative work, in the History of the Natural Sciences. Certain Phytohistorical studies or projects, which seem desirable from the point of view of the History of Science, as well as some needed from the entirely different viewpoint of the working botanist, are outlined. The differences and similarities between the methods of Cultural History and of Natural History are analyzed. Concluding remarks deal with certain international aspects of cooperative Phytohistorical studies.

The paper has been published in *Archives Internationales d'Histoire des Sciences*, 15, 1951, pp. 448-457.

SESSION 7

July 18th, 1—5 p. m., Attendance: 35 members

Chairman: R. C. ROLLINS, Recorder: E. HULTÉN

SUBJECT:

Various Papers

M. LEVYNS (London)

The Phytogeography of Polygalaceae in South Africa

Genera characteristic of the Cape Flora show a remarkable uniformity in the distribution of their species. The species are messed in the South West and the numbers diminish both northwards and eastwards.

Recent studies on *Muraltia*, an endemic genus of *Polygalaceae* with over 100 species, show that it has a marked concentration of species in the South West. The Kamiesberg form the northern limit in the West, but in the East one species reaches Tanganyika. Only about 1/10 of the species are widely distributed, and no species covers the whole area occupied by the genus. The number of species with very restricted areas of distribution is about 50 %, an unusually high proportion. Such species are found either at

fairly high altitudes on the mountains of the South West or close to the coast between the Cape Peninsula and Mossel Bay, part of the country which was covered by the sea in the Tertiary period. Striking discontinuities in distribution appear in a few species, viz.: *Muraltia macrocarpa*, *Muraltia alticola* and *Muraltia flanaganii*.

Mundia is another endemic genus, closely related to *Muraltia* and having a single species with a rather wider area of distribution than any single species of *Muraltia*.

Polygala, the remaining genus, is widely distributed throughout the world. Certain species are associated with the Cape Flora and do not extend beyond its area. The distribution of these species, however, is not that of typical members of the Cape Flora. There is no high concentration of species in the South West. In fact there are more species in the East than

in the West. Furthermore a high proportion of the species have a wide area of distribution and relatively few occupy limited areas. The differences between the genera are clearly brought out by the species occurring on the Cape Peninsula. There are 22 species of *Muraltia* of which 9 are endemic within this small area. 9 extend for a short distance beyond the Cape Peninsula and 4 are widely distributed. On the other hand *Polygala* has only 7 species of which not one is endemic and 5 are widely distributed.

Muraltia and *Polygala* are fundamentally different in their floral morphology and the genera appear to have evolved independently of one another. Their geographical distribution supports this. *Muraltia* is clearly a member of the Cape Flora while *Polygala*, though a common constituent, shows in its distribution that it is not a true member of that flora.

J. M. COWAN (Edinburgh)

On the Genus Rhododendron

Manuscript not received.

A. HÄSSLER (Lund)

The Group Cheloneae of the Genus Euphorbia

When making a monographic examination of some groups of the genus *Euphorbia* L., I have also been occupied with the group *Cheloneae*, distinguished and described by E. BOISSIER as a subsection of the section *Anisophyllum* (HAW) ROEP. BOISSIER mentions the following species as belonging to the group: *E. vaginulata* GRISEB., *nummularia* J. D. HOOK., *recurva* J. D.

HOOK., *flabellaris* N. J. ANDERSS., *apiculata* N. J. ANDERSS., *viminea* J. D. HOOK., *articulata* N. J. ANDERSS., *diffusa* J. D. HOOK., and *punctulata* N. J. ANDERSS. All these species with the exception of *E. vaginulata* are confined to the Galapagos Islands.

In connection with the discussion on the affinities and the limitation of the species I wish to point out that a herbarium specimen, described as annual, can be a first year plant of a perennial species. When a plant has been described as herbaceous, it may represent a young state of a fruticose plant. At the time of BOISSIER the material of all these species mentioned above was rather fragmentary as regards the variation of the species. For maintaining the different species mentioned by BOISSIER, this material therefore was more or less convincing. But when examining new rich material I have found plant individuals which seem to be combinations of species described as more or less herbaceous and their fruticose relatives.

According to my examinations of BOISSIER's 9 species of the group *Cheloneae*, the group ought to be diminished to the following 5 species: *E. vaginulata*, *viminea* (related to the preceding species), *nummularia*, *recurva*, and *diffusa*.

A preliminary note about this subject is published in "Botaniska Notiser" 1939.

P. CHOUARD (Paris)

Paysages botaniques des Pyrénées Centrales du Gavarnie à la réserve naturelle du Neouville

Manuscript not received.

SESSION 8

Jointly with Sections CYT, EXT and GEN: July 19th, 9 a. m. — noon, See page 277

SESSION 9

Jointly with Sections CYT, EXT and GEN: July 19th, 2—5 p. m., See page 277

SESSION 10

July 20th, 9 a. m. — noon, Attendance: 25 members

Chairman: A. E. PORSILD, Recorder: E. HULTÉN

SUBJECT:

Various Papers

R. FOSBERG (Washington, D. C.) *Functions of the Modern Herbarium*

Past is the time when a herbarium could fulfill its purpose by being a sample file of dried plant specimens with their labels, aiming to have one or more specimens of each kind growing in the area covered. The modern herbarium, in its fullest realization, is a vast living system for receiving, classifying, arranging, and storing information on plants, backed up by incontrovertible vouchers in the form of dried pieces of the actual plants themselves, and presenting it in usable convenient form when it is needed.

Clippings from literature, illustrations, drawings, photos, field notes, experimental results, vouchers for chromosome counts, for the changes effected in plants by physiological and genetical experimentation, as well as by horticultural selection, are all not only accepted but welcomed by those in charge of modern herbaria. These things add to the store of information about plants and their inherent variability, and are therefore of interest and value to the systematist, who has previously been considered the only one concerned with herbaria. This opportunity to use such a broad store of information makes the herbarium an institution of interest and utility to a great array of other types of botanists—geneticists, cytologists, physiologists, biogeographers, ecologists, plant breeders, horticulturists, economic botanists, and experimental taxonomists, as well as pure systematists. This must bring added support to the herbarium, as well as a healthy contact and exchange of ideas between all of these

groups of workers. In fact, one of the most important functions of the herbarium is as a meeting-place for botanists.

Discussion

H. J. LAM: We taxonomists and herbarium-workers have felt our hearts warmed by Dr. FOSBERG's words but I might suggest that he would repeat the same lecture before the physiologists etc., who have mostly but a very slight and primitive idea of the fundamental importance of our science.

G. CUFODONTIS (Wien) *Wilhelm Schimper, a Pioneer of Ethiopian Botany*

W. G. SCHIMPER's name is known to every botanist dealing with African Botany. But, as he never published anything, particulars of his life are still generally overlooked. His father was FRIEDRICH LUDWIG HEINRICH, a brother of the celebrated bryologist WILHELM PHILIPP, his mother MARGARETHE KATHARINA WILHELMINE, baroness VON FURTENBACH. Born at Reichenschwandt near Nürnberg on Aug. 2nd, 1803, primary school at Mannheim, apprenticeship for turner at Nürnberg, then until 1828 military service as quartermaster and sergeant in the Baden army. Then stay at München with his brother KARL FRIEDRICH, interested in Natural History, drawing and mounting fish skeletons for L. AGASSIZ. 1831 first botanical trip to S. France and N. Africa, interrupted in 1832 by illness. Till 1834 stay in Neuchâtel

with AGASSIZ and in Alsace with relatives. August 1834 start for Egypt in order to collect plants for the Württemberg Travel Association, founded by HOCHSTETTER and STEUDEL. After a shipwreck near Kephallonia and long delay arrival in Cairo, where his companion, Dr. WIEST, died of pestilence. 1835 collecting trip to Sinai. 1836 farewell to Egypt, January 1837 landing at Massawa and thence, after a short stay, proceeding to Assabot in Tigre, Abyssinia. Follow 3 years of diligent botanical exploration in Tigre and Semien, as a friend and guest of Ras UBIE. After a failed attempt to return to Europe, in 1840 definitive settlement in Abyssinia, marriage with a daughter of Ras UBIE and appointment as minister and governor of Anticho. 15 happy years of collecting activity for the Paris "Jardin des Plantes". 1855, because of Ras UBIE's ruin and imprisonment by Negus THEODOROS, loss of his offices, houses, goods and collections. Subsequent indigent life at Adowa with his son. 1868 prisoner of THEODOROS in Magdala, besieged by the British under Lord NAPIER. After the fall of the fortress return to Adowa and departure of his son to Europe, for Karlsruhe, Baden, in order to attend at the Polytechnical School, supported by a bursary of the Grand Duke of Baden. The rest of SCHIMPER's life passed in modest retirement on his little property at Adowa, but undisturbed. There he died in October 1878, just when his son, after an absence of 10 years, was coming back and going ashore at Massawa. In conclusion, an account is given of SCHIMPER's collecting spots and their geographical localization.

A full account of this lecture is published in *Phyton* 3 (1951) pp. 84—89.

A. PONCE DE LÉON Y AYMÉ (Habana)
*Contribution to the Phylogenetic
 Arrangement of the Dicotyledones*

This is an attempt at arranging the Dicotyledones into cohorts, taking into account phylogenetic considerations.

The existence of the so-called "Ranalic Com-

plex" that evolved before the Cretaceous and the remains of which are *Magnolia*, *Ranunculus* and *Nymphaea*, is accepted.

The predominance of the entomophily which is related to the euanctic plants and of the anemophily to the pseudantic plants are considered.

In the evolutionary process of the euanctic plants the following tendencies are stated:

- A. Enlargement of the receptacle to a hypanthium or transformation in a torus or thalamus.
- B. Reduction of the number of the sporophylls and symmetrical disposition to come to dorsiventral symmetry.
- C. Connation of the carpels to give an 1-celled ovary.
- D. Connation of the stamens and petals to get the metachlamideous condition.
- E. Clustering of flowers to form a climanthium.

According to the prevailing of some of these tendencies the following cohorts have been stated.

I. <i>Archicarpicae</i>	Ex. <i>Magnoliales</i>
II. <i>Calycicarpicae</i>	Ex. <i>Rosales</i>
III. <i>Syncarpicae</i>	Ex. <i>Geraniales</i>
IV. <i>Tubiflorae</i>	Ex. <i>Solanales</i>
V. <i>Umbelliflorae</i>	Ex. <i>Asterales</i>
VI. <i>Stephanocarpicae</i>	Ex. <i>Aristolochiales</i>
VII. <i>Myrtiflorae</i>	Ex. <i>Myrtales</i>
VIII. <i>Paracarpicae</i>	Ex. <i>Passiflorales</i>

In the pseudantic plants such tendencies (excepting those related to the petals) originate the three following cohorts:

IX. <i>Amentiferae</i>	Ex. <i>Fagales</i>
X. <i>Clinanthae</i>	Ex. <i>Urticales</i>
XI. <i>Centrospermae</i>	Ex. <i>Polygonales</i>

J. M. COWAN (Edinburgh)
The Royal Botanic Garden, Edinburgh

The Royal Botanic Garden, Edinburgh, was founded in 1670. Since its early days as a Physic-Garden with some 2000 medicinal plants arranged in formal beds it has grown to contain

a varied collection of some 35000 plants from every part of the world.

The Rock Garden with its unrivalled wealth of alpine plants is well known; the Woodland Garden, the Heath Garden, and Peat Walls, the Herbaceous Border and the Arboretum are among the more outstanding features; the range of Plant Houses and Propagating Department are also of interest.

The lecture was illustrated by coloured views of the Garden and some of its noteworthy plants.

E. M. HERING (Berlin)

Die Oligophagie phytophager Insekten als Hinweis auf Pflanzenverwandtschaften

Unter den phytophagen Insekten sind Blattminierer für folgende Untersuchung besonders geeignet, da sie meist ihre Gesamtentwicklung in einem Blatt durchmachen und die Pflanze nicht wechseln können; sie sind in der Regel monophag; jede Art lebt auf einer bestimmten Pflanzengattung. Polyphagie, Vorkommen wahllos auf verschiedenen, nicht verwandten Familien, ist selten. Normalem Vorkommen (Euphagie) steht Xenophagie, ausnahmsweises Vorkommen an anderer, nicht verwandter Pflanze gegenüber. Zwischen Monophagie und Polyphagie steht die Oligophagie, Vorkommen an einigen Gattungen gleicher oder verschiedener Familien. Da die Nahrungsauswahl der Larve sich auf das von ihr nur zur Ernährung verwendete Eiweiss bezieht, gibt die Oligophagie Hinweise auf die Verwandtschaft der Eiweisse der gewählten Gattungen und damit auf die Verwandtschaft der Wirtspflanzen.

Bei der systematischen Oligophagie sind die ausgewählten Pflanzengattungen \pm miteinander verwandt. Oligophagie 1. Grades (Larve beschränkt sich auf Gattungen der gleichen Pflanzenfamilie) ist sehr häufig. 2 Arten von Minierern (und ebenso Blattläuse) leben an *Aconitum* und *Delphinium*; dass wieder 2 Arten (und ebenso Aphididen) an *Thalictrum* und *Aquilegia* leben, lässt auf nähere Verwandt-

schaft beider schliessen. Bei Oligophagie 2. Grades leben Arten an und nur an Gattungen verschiedener Familien der gleichen Ordnung (viele Arten an Cruciferen, Resedaceen und Caparidaceen). Nahrungsauswahl bei der Oligophagie 3. Grades bezieht sich auf Gattungen verschiedener Familien aus verschiedenen Ordnungen. Eine *Gracilaria* lebt an *Chenopodiaceae*, *Polygonaceae* und *Primulaceae*. Das Vorkommen einer Fliegengattung und von *Elachista* (*Lepidoptera*) an und nur an Glumifloren und *Juncaceae* wie auch identischer *Chylizosoma* (*Diptera*) an *Liliaceae* und *Orchidaceae*, der Fliedermotte an *Oleaceae* und *Symphoricarpos*, lässt auf nähere Verwandtschaft der befallenen Pflanzenfamilien schliessen, als sie im System zum Ausdruck kommt. Das Vorkommen von 2 Artengruppen der Minierfliegengattung *Phytomyza* wie auch sämtlicher minierender Fruchtfliegen der Holarktis auf Compositen und Umbelliferen weist auf Beziehungen zwischen diesen Familien hin.

Bei der disjunktiven Oligophagie lebt eine Art an verschiedenen, wenigen Gattungen nicht näher verwandter Familien. Das kann auf „Dunstkreis“ der Pflanzen im gleichen Biotop (*Lyonia* *ledi* Wck. an *Ledum* und *Myrica*) zurückgeführt werden und wird vielfach die Möglichkeit einer fernerer Verwandtschaft offen lassen. Alle *Antispila*-Arten (*Lep.*) leben an *Cornaceae* und *Vitaceae* (beiden das „Weinrot“ gemeinsam). Auffallend gross ist das gemeinsame Vorkommen vieler Arten an und nur an *Rosaceae* und Familien der *Amentiferae*, das vielleicht doch auf verwandtschaftliche Beziehungen beider hinweist. Mehrfach zu beobachtende Oligophagie an Gattungen der *Centrospermae* und solchen der *Solanaceae-Gentianaceae* lassen auch hier ähnliche Beziehungen vermuten, die Annahme der polyphyletischen Entstehung der *Sympetalae* stützend.

Wie bei parasitären Pilzen werden auch hier „bridging species“ beobachtet; wie bei diesen ist auch hier *Tropaeolum* eine Gattung, über die den Arten der Übergang von Cruciferen auf Centrospermen und vice versa ermöglicht. H. BUHR stellte als weitere „bridging

species" *Antirrhinum majus* L., *Lupinus albus* L., *Lallematia* und *Helipterum* fest.

Oligophagie gibt keine Beweise, aber Hinweise auf Möglichkeiten von Pflanzenverwandtschaften, die mit Methoden der Pflanzenverwandtschafts-Forschung noch nicht erfasst werden konnten.

Discussion

W. T. STEARN: The indications of a relationship between plants afforded by the preference etc. of leaf-mining insects are comparable with those afforded by certain fungi and may be presumed to rest on certain biochemical resemblances between these host plants. A natural system of classification, though based primarily on morphology, aims to group together plants agreeing in the sum of their characters, which will include biochemical ones. Certain morphological characters appear to be the same in apparently unrelated groups, and the independent syntheses of similar substances in unrelated plants may be an explanation of the peculiar diversity of hosts shown by certain of the examples named.

H. J. LAM (Leyden)

Concluding Remarks

Before we leave, may I say a few words to conclude the discussions in this section. First of all I deem it a pleasant duty to extend our thanks and to express our warm appreciation to the man who made everything in our lectures run smoothly. I mean, of course, our recorder Dr. HULTÉN. We all know, Dr. HULTÉN, that you are, as director of a large and important botanical institute, a very busy man. We have noticed, as a sign of your well-known activities,

your magnificent Atlas of the Distribution of Scandinavian Plants, which has just appeared and on which I think we must congratulate you sincerely.

Knowing all this our appreciation for what you did as recorder of this section is only the greater and I may invite the audience to express our feeling by a hearty applause.

Furthermore I may recall that four vice presidents were, at my request, kind enough to take the chair of the section for one of the meetings. Personally I want to tender my thanks for their co-operation to Dr. TURRILL, Dr. RECHINGER, Dr. ROLLINS and Dr. PORSILD.

I hope that in the intercongressional period before us, international conditions will enable us to continue our work, which is mostly referred to as peaceful. Of course, in comparison with some other human activities, our work is peaceful, though sometimes this peace is of the nature of that which is supposed to have reigned in the family of Adam and Eve. For brotherly feelings among scientists are, it seems to me, sometimes not very far from those between Cain and Abel.

However, such was not the case in the meetings and in the discussions of this section, which brought us together in an atmosphere of perfect friendship. I wish to thank everybody for this and I add my sincere thanks to all those who read or contributed a paper or took part in the discussions.

I think that in general our work has been successful. I wish you all the best of times both in your work and in your personal lives, and I may express the hope that we will meet at the next Congress in good health and under happy conditions. With these words I declare the meetings of the Section for the Taxonomy of Phanerogams adjourned.

PALYNOLOGICAL CONFERENCE

President: F. FIRBAS

Vice-Presidents: H. GODWIN, H. A. HYDE, R. POTONIÉ

Recorder: G. ERDTMAN

Vice-Recorder: O. HEDBERG

SESSION 1

July 10th, 9.30 a. m. — noon, Attendance: 55 members

Chairman: F. FIRBAS, *Recorders:* G. ERDTMAN and O. HEDBERG

SUBJECT:

*Pollen Morphology, Pollen Morphology and Plant Taxonomy (Coniferae),
Palynological Aspects of Melitology*

G. ERDTMAN (Stockholm) and F. FIRBAS (Göttingen)

Opening Remarks

In introducing the President, Professor F. FIRBAS, the Recorder mentioned that it was only a few weeks ago that it was decided to organize the Palynological Conference in the same way as the Sectional Meetings. It was then too late to incorporate all palynological subjects in the Palynological Conference. Some subjects will, therefore, be dealt with in the section of experimental ecology and others in the section of phytogeography.

Professor F. FIRBAS in opening the meeting called attention to the pioneer work of Swedish botanists in the science of palynology. He also lamented the recent death of Professor B. SAHNI, Lucknow.

J. IVERSEN (Köbenhavn)

Identification of Difficult Pollen Types by Means of Structural Characters

When pollen statistical research was initiated, the first task was to provide a survey of the

principal phases of forest development, and so it was sufficient to count the pollen of the most important forest trees, which, with certain exceptions, are easily recognizable. To-day this state of things has changed. The first object of pollen analysis has been attained; to proceed, it is necessary to consider the pollen of the other plants as well. Only on that base a deeper comprehension of the vegetational development and its causes can be expected.

Obviously the new aspect of pollen analysis demands very careful attention to pollen morphological questions. Especially, the structure of the exine should be studied more thoroughly. A close examination of structural details, in fact, enables us to make reliable determinations of pollen grains that cannot be identified by usual means.

In principle, the structure of the pollen exine was cleared up by FRITZSCHE, and I think his conception is still valid. According to FRITZSCHE the basic elements of the exine are the "Körnchen" (granules), which are embedded in, or adhere to, a homogeneous matrix. One can distinguish between open and closed struc-

ture. In the case of an open structure ("intectate"), the granules, adhering to the homogeneous endexine, are more or less mutually detached, or unified laterally only, forming an open network. Structure and sculpturing are then identical. In the closed structure ("tectate") the granules are thickened at their uppermost ends, meeting, or almost meeting, forming an outer sheet ("tectum"). In this case the sculpturing is confined to the features of the tectum and not consistent with the structure of the exine. By distinguishing between open and closed structure pollen of equal sculpturing type are divided into two classes. A closed structure is found, e.g., in the reticulate pollen grains of many *Labiatae* and *Leguminosae*, while the reticulum of e.g. the pollen of *Liliales* and *Cruciferae* is open. Of great diagnostic value is the structure of the protuberances of the exine; in some cases these are one single granule (e.g. *Populus*, *Ilex*); in other cases they are composed of quite a number of granules (e.g. the spines of the *Tubuliflorae*).

We may illustrate the practical use of these characters by one example. *Populus* pollen seems to have been ignored hitherto in pollen analysis, obviously because of its similarity to the pollen of *Cyperaceae*. However, *Populus* pollen is intectate, while *Cyperaceae* pollen is tectate. By means of this character and an immersion objective *Populus* pollen is easily counted in all sediments.

Discussion

G. ERDTMAN: Some sporoderm details can be successfully studied with the electron microscope.

F. FIRBAS: Das Phasenkontrast-Mikroskop (wir benützen ein solches von Zeiss-Winkel, Göttingen) leistet bei dünnwandigen Pollen zum Erkennen der Struktur und Skulptur sehr gute Dienste. Mein Mitarbeiter G. LANG versuchte damit neuerlich die Unterscheidung der Pollen von *Pinus Mugo* (*montana*) und *P. silvestris*—freilich mit dem Ergebnis, dass die bisher für wesentlich gehaltenen Unterscheidungsmerk-

male der beiden Arten (je nach der Herkunft des Materiales) wechselnd auftreten können. Bei dickwandigen, weniger lichtdurchlässigen Pollen dürfte das Phasenkontrastverfahren weniger brauchbar sein.

R. POTONIÉ: Der Vortrag von Herrn IVERSEN zeigt wieder einmal, was ich schon mehrmals betonte, wie sehr wir gerade bei den fossilen Pollen die Struktur- und Skulpturverhältnisse der Exine berücksichtigen müssen. Im Grossbau einander entsprechende Formen werden durch das exakte Studium der Exine unterscheidbar.

H. STRAKA (Bonn)

Untersuchungen über *Salix*-Pollen

Auf Anregung Dr. ERDTMANS versuchte ich, morphologische Feinmerkmale zur Unterscheidung des Pollens aller mitteleuropäischen und skandinavischen *Salix*-Arten heranzuziehen. Die Präparate wurden fast alle aus Herbarmaterial des Naturhistoriska Riksmuseet, Stockholm, hergestellt.

In ERDTMANS Introduction (1943, S. 121) findet sich eine Beschreibung des *Salix*-Pollens. Da in dem Colpus eine Pore (Os) angedeutet ist, zählt man ihn zu dem colpoiden Typus. Jede Masche der Retikulierung wird als *Brochus* bezeichnet und besteht aus erhabenen, bei hoher Einstellung hellen marginalen Murusanteilen, die das zentrale Lumen umschliessen.

Mit Hilfe verschiedener Eigenschaften kann man 6 Arten (*Salix glabra*, *silesiaca*, *herbacea*, *daphnoides*, *pentandra*, *alba*) von den übrigen unterscheiden, die zu zwei Gruppen zusammengefasst werden. Genaue Anweisungen über die Einstellung des Pollenkornes sind zu beachten. Wenn man feststellen will, ob die Retikulation bis an den Colpus-Rand reicht oder nicht, so ist dieser so einzustellen, dass er genau den "Mittlermeridian" des Pollenkornes bildet. Zur Feststellung der *Brochus*-Grösse verwendet man die auf dem zentralen Teil der intercolparen Fläche gelegenen Brochi, indem man so einstellt, dass der "Mittlermeridian" des Pollenkornes mit der Mittellinie der intercolpa-

Morphologisch unterscheidbare Gruppen von *Salix*-Pollen

		A. Die Retikulation endet vor dem Colpus-Rand	B. Die Reticulation reicht bis an den Colpus-Rand
I. Brochi untereinander von ziemlich gleicher Grösse, nur verhältnismässig wenige anders als die übrigen.	a. Brochi gross oder gross bis mittelgross (weit- und weit- bis mittelmaschige Typen).	nur ohne Flecken in den Lumina: <i>silesiaca</i>	α) mit Flecken in den Lumina: <i>glabra</i> β) ohne Flecken in den Lumina: <i>arbuscula</i> , <i>depressa</i> ssp. <i>livida</i> , <i>glauca</i> , <i>grandifolia</i> , <i>myrsinites</i>
	b. Brochi mittelgross bis klein (mittel und feinmaschige Typen) Lumina zeigen kleine Flecken.	1. Brochi von mehr unregelmässiger Gestalt: <i>herbacea</i> 2. Brochi von ziemlich regelmässiger Gestalt: <i>daphnoides</i>	21 Arten
II. Brochi mit sehr unterschiedlichen Grössen, grosse und kleine gemischt, die grossen Lumina meist mit Flecken.		die kleinen Brochi sind vorwiegend in Gruppen gestellt: <i>pentandra</i>	vorwiegend einzelne kleine Brochi: <i>alba</i> .

ren Fläche zusammenfällt. Eine übersichtliche Tabelle wurde ausgearbeitet, aber darauf hingewiesen, dass ein eingehendes Studium von Präparaten rezenter Pollen nötig ist.

Da in den Präparaten jeder Art ein kleiner Teil abweichender Pollenkörner vorkam, scheint man rezenten und fossilen *Salix*-Pollen nach seiner Herkunft nur dann sicher bestimmen zu können, wenn der Typus in höheren Prozentzahlen auftritt.

Es wurden 6 ausgewählte *Salix*-Bastarde geprüft. Der Typus eines Elternteiles pflegt zu überwiegen. Häufig sind Missbildungen, selten Neukombinationen. *Salix*-Bastarde sind also pollenanalytisch kaum feststellbar. Sie dürften keine wesentliche Fehlerquelle bei pollenstatistischen Untersuchungen darstellen.

14 untersuchte salicoide Pollenarten können alle durch wenigstens ein pollenmorphologisches Merkmal von *Salix* unterschieden werden. *Artemisia* und *Fraxinus* sind kaum noch als

salicoid zu betrachten. Beide mitteleuropäischen *Evonymus*-Arten und *Parnassia* sind deutlich tricolporat. Verschiedene andere Merkmale scheiden die drei *Sambucus*-Arten, *Viburnum*, *Adoxa*, drei untersuchte *Verbascum*-Arten, *Diapensia*, und *Tamarix* gut von *Salix*. *Saxifraga stellaris* (von den untersuchten Arten der Gattung nur diese) ist wohl am *Salix*-ähnlichsten, lässt sich aber auch von dieser unterscheiden.

Wir haben früher in Bonn bearbeitetes fossiles Material, das reich an *Salix* war¹, mit Hilfe der hier gewonnenen Erfahrungen auf die Arten hin nachzubestimmen versucht. Die zwei untersuchten Proben liegen etwas vor dem *Salix*-Maximum. Etwa 1/3 der *Salix*-Pollen war unbestimmbar; von den gut erhaltenen wurden 100 Stück prozentual ausgezählt. Es ergab sich, dass *Salix pentandra* einen wesentlichen

¹ FRECHEN, J. und STRAKA, H., Die Naturwissenschaften 37/8, 1950.

Anteil der beschriebenen Pioniervegetation gestellt haben muss.

Auf die Möglichkeit einer Variation der Pollen verschiedener geographischer Herkünfte der gleichen Art wird hingewiesen, worüber aber keine Untersuchung gemacht werden konnte.

Discussion

J. IVERSEN: The pollen grains of *Saxifraga stellaris* var. *comosa* are difficult to distinguish from those of *Salix*. The grains of the former come much nearer to *Salix* pollen than to those of the main species *Saxifraga stellaris*. I agree with Mr. STRAKA that *Salix herbacea* pollen can be identified rather safely. It is, however, not very frequent in Danish Late-Glacial deposits.

P. THOMSON: Weidenbastarde spielen mengenmässig oft eine grössere Rolle als die reinen Arten, daher dürfte auch der Pollen von Weidenhybriden fossil weit verbreitet sein. *Salix pentandra* blüht viel später als alle anderen Weidenarten (in Estland oft Ende Juni) und kann daher schwer Bastarde bilden. Ich habe diese Art immer in der reinen Form beobachtet.

MADELEINE VAN CAMPO-DUPLAN (Paris)

Du terme «sillon» dans la nomenclature palynologique

Le terme «sillon» (furrow, Furche), d'un usage courant en Palynologie, est la source de confusions regrettables par le fait qu'il désigne tantôt un pli sur un grain de pollen, tantôt une disposition de l'exine à laquelle une valeur phylogénique considérable est attribuée.

Voici quelques citations se rapportant à la morphologie ou à la valeur phylogénique du sillon: d'après la définition «a germinal furrow is a longitudinal groove or opening in the exine, either enclosing a germ pore or serving directly as the place of emission of the pollen tube, also generally serving as a harmomegathus». Pour un grain de pollen à ballonets on trouve la définition suivante: «The intervening space between the bladders is, morphologically speaking, the furrow which in *Pinus* and similar types ex-

tends from end to end of the grain, vertical to the plane which passes through the two bladders».

Sur l'importance phylogénique du «sillon» nous lisons encore que les *Cycadofilicales* possèdent de profonds sillons «which became so prevalent and came to play so important a role in the evolution of the pollen grains of all later Gymnosperms»; et: «The evolution of the pollen grains of all the surviving descendants of the *Cordaitales*, except *Ginkgo*, was accompanied by a modification, protection or elimination of the very furrow which was the great achievement of the Cordaitalean pollen grains.»

Cette dénomination de sillon est d'ailleurs maintenant l'apanage des Gymnospermes puisque pour les Angiospermes les termes sulcus, colpus, ruga, porus, etc. ont été définis.

Chez les Conifères les grains de pollen sont organisés sur deux types différents, l'un avec sac à air, l'autre sans sac à air, mais ces deux types ont en commun le caractère d'émettre leur tube pollinique en un endroit imprécisé de leur partie distale où leur exine fine se déchire; de plus ils fonctionnent tous sur le même mode, c'est à dire qu'ils invaginent, lorsqu'ils sont dans l'atmosphère leur partie distale dans leur partie proximale. Toutes les superstructures du grain de pollen se trouvent entraînées dans ce mouvement; si le pollen a deux ballonnets ceux-ci se trouvent rapprochés et un pli se forme entre eux; si le pollen a trois ballonnets l'invagination entraîne le même rapprochement des trois ballonnets; si le grain possède un seul sac à air une invagination en forme de cuvette se produit à l'endroit où l'exine est fine, c'est à dire à la partie distale du grain; si le grain ne possède aucun système anémochorique il est sphérique et sa partie distale s'incurve dans sa partie proximale. La forme du système anémochorique du grain conditionne donc la symétrie du pollen et par conséquent détermine la forme de sa zone germinale.

On ne peut nier que les parties distales d'un pollen de Pin à deux ballonnets, d'un pollen de *Microcachrys* à trois ballonnets, d'un pollen de *Tsuga* à un seul sac à air, d'un pollen de *Pseudo-*

tsuga n'ayant plus trace de sac à air, sont des formations phylogénétiquement comparables. Cette identité n'est pas exprimée lorsque l'on dit que les pollens à deux ballonnets ont un sillon ayant un rôle important dans l'évolution, et que les autres pollens de Conifères n'en ont pas.

On a invoqué pour parler de « sillon » chez les *Podocarpus* par exemple, le fait que la zone germinale était souvent bordée par un bourrelet à la racine distale des ballonnets. Mais, et la chose est très nette chez *Podocarpus ferrugineus*, le bourrelet se trouve aussi bien à la racine proximale qu'à la racine distale des ballonnets.

Une autre raison plus simple et plus péremptoire montrant que le terme sillon, tel qu'il est défini, est vicieux lorsqu'il est appliqué aux Conifères est la suivante: un sillon est par définition un pli longitudinal sur un grain de pollen¹, or, dans le cas des pollens à deux ballonnets il n'y pas de sillon longitudinal puisque l'axe de la zone germinale se trouve toujours dans le plan perpendiculaire en son milieu au grand axe des pollens. Les grains de pollen des Conifères ont donc comme caractère commun de ne jamais posséder de sillon au sens de la définition du terme.

En conclusion, si l'on peut parler de sillon, furrow, Furche, pour les grains de pollen des Conifères c'est uniquement dans le sens de pli sur les pollens. Pour comparer ces pollens phylogénétiquement on est amené à parler d'une zone germinale, si l'on veut un terme qui puisse désigner à la fois toutes les formes de la zone germinale quand le grain est sec il semble que l'on puisse choisir invagination ou, pour être dans la ligne de porus, ruga, colpus, sulcus, etc. le terme incurvatio peut être proposé.

MADELEINE VAN CAMPO-DUPLAN (Paris) Pollens et phylogénie chez les Conifères

Il est sans doute ambitieux de parler de lois de l'évolution pour les grains de pollen, néan-

¹ Le terme « transverse furrow » a été défini mais il s'agit d'une formation bien différente en effet le « sillon transverse » est toujours associé à un sillon; son stade de réduction final étant un pore au centre du sillon germinal.

moins des tendances peuvent être soulignées, les caractères qui ont une importance majeure pour l'étude de l'évolution des Conifères seront seuls considérés ici.

Les comparaisons de taille des grains de pollen ont une grande signification en phylogénie.

Chez les Angiospermes les auteurs sont à peu près tous d'accord pour considérer comme évoluées, entre autres, les familles suivantes: Dipsacacées, Polémoniacées, Oenothéracées, Plumbaginacées, Cucurbitacées, Violacées, Malvacées, Iridacées... ces familles ont toutes des grains de pollen de dimensions considérables. Toutefois ce caractère taille doit être manié avec précautions et on ne peut conclure qu'une famille n'est pas évoluée par le seul fait qu'elle possède de petits pollens. Des facteurs, qui ne sont pas évolutifs, influent sur la taille des pollens, ce sont les facteurs qui provoquent des meioses anormales, mais ces facteurs agissent accidentellement et leur action est négligeable dans des études d'ensemble. On peut se demander si le milieu, qui peut avoir une importance considérable sur l'aspect des végétaux, peut modifier la morphologie des pollens. Des travaux sur les grains de *Pinus echinata* permettent de penser que le milieu peut influencer sur la taille des pollens, mais seulement dans certaines limites, les variations étant de l'ordre d'une dizaine de microns dans les cas les plus extrêmes.

Nous pouvons poser en principe que, à l'intérieur d'un phylum, la taille des grains de pollen augmente au cours de l'évolution.

De nombreuses espèces de Conifères ont des grains de pollen possédant un sac à air. On retrouve cette disposition dans le pollen des Cordaitales. R. FLORIN a montré que ce sac à air avait diminué de volume au cours des périodes géologiques, un accolement des parois de l'exine s'étant réalisé peu à peu à la partie proximale des grains de pollen; il en est résulté des grains portant deux ou trois ballonnets. Des grains de pollen actuels peuvent également donner des indications précieuses sur les variations du sac à air, ce sont les pollens des hybrides; ainsi certains pollens possédant normale-

ment deux ballonnets ont pu montrer un vaste sac à air unique, trois ballonnets ou une regression presque compète de la calotte et des ballonnets. Les grains de pollens anormaux trouvés dans les charbons et les tourbes sont très vraisemblablement des pollens d'hybrides.

L'étude des pollens d'hybrides a une importance réelle en phylogénie, elle a permis notamment de montrer que les *Tsuga* aberrants possédant des ballonnets étaient en réalité des hybrides entre des *Tsuga* et des espèces d'autres genres d'Abiétacées, *Keteleeria* et *Picea*, donc des hybrides intergénériques.

Quelles conclusions peut-on tirer de l'étude de leurs pollens pour établir une classification phylogénique des Conifères?

Les Conifères comprennent des familles possédant surtout des grains de pollen à ballonnets: Abiétacées, Podocarpacees et des familles ne possédant jamais de pollen à ballonnets: Araucariacées, Cupressacées, Taxodiacees, Céphalotaxacées, Taxacées.

Les recherches sur la morphologie des grains de pollen permettent d'établir à l'intérieur de ces familles une classification naturelle des genres, même des espèces.

Les grains de pollen des Abiétacées ou Pinacées se divisent en: grains de pollen possédant un système anémochorique comprenant les grains de pollen à ballonnets des genres *Pinus*, *Cedrus*, *Pseudolarix*, *Keteleeria*, *Abies*, *Picea*; les grains de pollen sans ballonnets du genre *Tsuga* et en: grains de pollen sans système anémochorique des genres *Larix* et *Pseudotsuga*.

Quelles conclusions la loi de croissance de taille des grains de pollen permet-elle de déduire?

Le genre *Pinus* est celui qui possède les plus petits pollens. On peut donc penser qu'il est le plus primitif de la famille. Cette hypothèse est d'ailleurs confirmée par l'étude de très nombreux caractères.

Les genres *Pseudolarix* et *Keteleeria* ont des grains de pollen tout à fait comparables, les grains de pollen de *Keteleeria* étant nettement plus gros, nous pouvons établir la parenté *Pseudolarix* → *Keteleeria*.

Le genre *Cedrus* ayant des pollens relativement petits est primitif.

Le genre *Abies* possédant de gros pollens est évolué.

Le genre *Picea* a des pollens souvent très gros, leur exine est semblable à celle des Pins ce qui permet de penser que le genre *Picea* est issu du genre *Pinus*.

Dans les genres qui suivent le sac à air s'est réduit considérablement, il n'en reste qu'un fin bourrelet dans le genre *Larix* et il est disparu complètement dans le genre *Pseudotsuga* qui est très évolué pour ce caractère. Les grains de pollen sans ballonnets ont pu dériver des grains de pollen à ballonnets, les grains de pollen des hybrides nous montrent sur des exemples vivants la possibilité de cette évolution, nous pouvons donc établir la parenté *Pinus* → *Larix* → *Pseudotsuga*.

Le cas des *Tsuga* (*Eutsuga*) est un peu plus compliqué à envisager, ces pollens ne portent pas trace de ballonnets mais seulement une calotte à bords souvent épaissis, cette forme de pollen paraît dériver d'une forme à sac à air unique et non d'une forme à deux ballonnets, toutefois l'étude des hybrides a montré la grande plasticité du sac à air, et la seule existence de ce sac à air unique des *Tsuga* ne permet pas de les séparer profondément des autres Pinacées d'autant plus que nous avons déjà constaté la formation d'hybrides intergénériques fertiles entre des *Tsuga* et des *Keteleeria* ou des *Picea*, ce qui indique une parenté entre les genres. La petite taille des pollens en fait toutefois un genre primitif.

L'intérêt que présente les recherches phylogéniques par les grains de pollen dans l'étude des genres d'une famille peut même se soutenir lorsque l'on aborde l'étude des espèces d'un genre. Le genre *Pinus* s'est montré très significatif à cet égard.¹

Les Podocarpacees, quoiqu'ayant des grains de pollen à ballonnets ont eu certainement une histoire assez différente de celle des Abiétinées.

¹ Voir: M. VAN CAMPO-DUPLAN: Recherches sur la phylogénie des Abiétinées d'après leurs grains de pollen. Thèse de doctorat Toulouse 1950.

En effet chez cette dernière les parentés étaient toutes visibles à partir du genre *Pinus*, les *Tsuga* mis à part; chez les Podocarpacees au contraire, nous nous trouvons devant une série de formes dont il est difficile de dire quelle est la plus primitive et la plus évoluée; il semble bien toutefois que la forme la plus primitive du genre soit un *Dacrydium* à petits pollens et à vaste système anémochorique comparable à *Dacrydium araucarioides*; à partir de cette forme de base deux courants évolutifs se seraient manifestés. Un premier courant suivant la loi d'augmentation de taille et comprenant certains *Dacrydium* et tous les *Podocarpus* et un second courant suivant la loi de régression du sac à air et comprenant les genres *Microcachrys* et *Pherosphaera* à trois ballonnets, la symétrie d'ordre trois est fréquente dans cette famille, et les genres *Phyllocladus* et *Saxegothaea*, tout sac à air ayant complètement disparu dans ce dernier genre. Les données polliniques semblent indiquer que les Abiétacées et les Podocarpacees ont évolué à partir de deux groupes différents de Cordaitales, l'un dans l'hémisphère Nord, l'autre dans l'hémisphère Sud. Les Podocarpacees semblent être apparues les premières, nous les trouvons aujourd'hui plus diversifiées et plus fragmentées à l'image de leur aire de répartition.

Parmi les familles dont le pollen ne possède jamais de ballonnets ce sont les Araucariacées qui ont les plus gros pollens et les ornements les plus épaisses. Les Araucariacées sont donc des arbres probablement très évolués; cette conception apporte une confirmation aux travaux récents faits sur ce groupe.

La famille des Taxodiacees est caractérisée, pour la majorité de ses genres, par un pollen subsphérique portant à sa partie distale une papille formée d'une exine très mince. Les genres *Cunninghamia* et *Sciadopitys* occupent dans cette famille une place à part, ils possèdent de gros pollens.

La famille des Cupressacées pose un problème assez troublant, en effet tous ses pollens semblent identiques à de petites variations de taille près. Cette famille a cependant donné lieu à

toute une classification en sous-familles, genres et même sous-genres, mais l'enigme de son évolution semble tout à fait impenétrable pour le palynologue.

Avec les Taxacées et les Céphalotaxacées nous touchons également à un problème délicat, ces deux familles ont des grains de pollen semblables, ceux des Céphalotaxacées étant plus gros que ceux des Taxacées; ce sont des pollens subsphériques ayant une zone germinale petite, circulaire et bombée, tenant en somme le milieu entre la papille des Taxodiacees et l'absence de zone germinale différenciée des Cupressacées. Les seuls caractères de l'enveloppe des pollens ne nous donnent pas ici d'indications de premier ordre sur l'évolution de ces familles, d'éminents botanistes ayant séparés profondément le groupe des Taxales des Conifères.

Après avoir acquis une vue d'ensemble très schématique sur le pollen des Conifères, essayons, d'après leur seul grain de pollen, de relier ensemble les familles de ce groupe, cette étude a déjà été faite mais je voudrais essayer de la reprendre en donnant au caractère taille sa vraie valeur et en négligeant la notion de sillon qui est à mon avis fallacieuse.

La possession d'un sac à air a marqué le groupe des Cordaitales et leur descendance mais nous avons pu constater la plasticité de cette formation, et les deux grandes familles qui possèdent des pollens à ballonnets, les Abiétacées et les Podocarpacees comprennent des genres ayant perdu toute trace de sac à air, cette perte des ballonnets étant une des voies de l'évolution dans ces groupes.

Les Cordaitales furent au Permien en particulier, un groupe extrêmement important comprenant différents types comme le souligne R. FLORIN, il semble donc que l'on puisse formuler l'hypothèse raisonnable que les Cordaitales devaient renfermer des groupes dont les pollens avaient déjà évolué vers la perte des ballonnets, de ces groupes sont issues les familles dont les pollens ne portent jamais de sac à air, ces familles présentent donc dès leur origine certains caractères évolués.

Cette étude tend à montrer que la palyno-

logie, dont le domaine s'étend de plus en plus, offre entre autre l'avantage de fournir au systématicien un outil de grande valeur pour ses recherches sur la classification phylogénique des plantes.

Discussion

P. THOMSON: Le pollen de *Cedrus* est très rare dans les couches néogènes de l'Allemagne du N.-Ouest mais il se trouve surtout dans le Pliocène inférieur. Dans les préparations de pollen récent pris sur des arbres cultivés à Bonn je remarquais toujours que les ballons du grain sont d'une forme très irrégulière.

M. VAN CAMPO-DUPLAN: Ces arbres doivent être d'origine hybride.

G. ERDTMAN: Mme VAN CAMPO has demonstrated that there is no insurmountable gap between the pollen types of *Larix* and *Pseudotsuga* on the one hand and those of *Pinus* etc. on the other. This is also interesting from a purely morphological point of view.

ANNA MAURIZIO (Liebfeld-Bern)

Pollenanalyse des Honigs

Die Pollenanalyse des Honigs diene ursprünglich dem praktischen Zweck einer einwandfreien Überwachung des Honigmarktes. Länder mit hohen Produktionskosten sahen sich gezwungen, zum Schutze ihrer Landwirtschaft eine obligatorische Herkunftsdeklaration für landwirtschaftliche Produkte, darunter Honig, einzuführen. Ein wirksamer Schutz der einheimischen Honigproduktion ist nur möglich, wenn man über eine zuverlässige Methode der Herkunftsbestimmung verfügt. Die Pollenanalyse bietet bisher die einzige objektive und sichere Möglichkeit zur Ermittlung der geographischen Herkunft von Honig.

Die mikroskopische Honiguntersuchung basiert auf der Tatsache, dass jeder Naturhonig pflanzliche Bestandteile enthält, die schon auf der Pflanze in die Rohstoffe (Nektar, Honigtau) gelangen und im reifen Honig nachweisbar sind. Der Nektar ist charakterisiert durch Pollen-

körner der von den Bienen besuchten Pflanzen; der Honigtau durch grüne Algen, sowie durch Sporen von Russtaupilzen, welche aus der Oberflächenflora der Waldbäume stammen. Die Bestimmung und Auszählung der im Honigsediment enthaltenen pflanzlichen Bestandteile erlaubt eine Rekonstruktion der Pflanzengesellschaft, in welcher der Honig von den Bienen gesammelt wurde und damit die Bestimmung seiner geographischen Herkunft. Die Bienen treffen in der sich ihnen anbietenden Pflanzenwelt eine bestimmte Auslese, die zur Bildung charakteristischer Pollenkombinationen, sog. „Honigtypen“, führt, welche eine Lokalisierung der Herkunft erleichtern.

Auf gewisse Schwierigkeiten stößt die Pollenanalyse noch, wenn es sich darum handelt, die Honigflora eines Landes oder den Wert einer Pflanze als Honigliefertantin auf Grund des Pollenbildes des Honigs zu beurteilen. Soll die Pollenanalyse auch auf diesem Gebiete brauchbare Ergebnisse zeitigen, so müssen folgende Fragen noch besser abgeklärt werden:

1) Können Pollenkörner auf anderem Wege als durch den Nektar in den Honig gelangen? Welchen Weg nehmen z. B. die im Honigsediment vorkommenden Pollenkörner von Windblütlern und nektarlosen Pollenblumen?

2) Welches Verhältnis besteht zwischen dem im Honigsediment gefundenen prozentualen Anteil einzelner Pollenformen und dem Anteil Nektar, mit welchem die betreffenden Pflanzen an der Entstehung des Honigs beteiligt sind? Lassen sich Normen aufstellen für die Pollenmenge, die bei den einzelnen Pflanzen in die Einheit Nektar gelangt?

3) Hat die in der Honigblase der Biene vor sich gehende Pollenreduktion Einfluss auf den absoluten Pollengehalt und das gegenseitige Verhältnis der Pollenformen im Honigsediment?

4) Welche Bedeutung kommt den im Honigsediment enthaltenen Algenzellen und Russtaupilzen zu? Kann die Herkunft des Honigtaus von verschiedenen Waldbäumen auf Grund der Pilzsporen-Formen bestimmt werden? Sind die Algen ebenso zuverlässige Honigtauzeiger wie die Russtaupilze oder ist ihr Vorkommen im

Honigsediment von klimatischen Faktoren abhängig?

5) Wie wirkt sich die Honiggewinnung und -Behandlung auf den Pollengehalt und das Verhältnis der Pollenformen im Honigsediment aus?

Discussion

F. FIRBAS: Leider hat bisher nur ein geringes Zusammenarbeiten zwischen Pollenanalytikern

und Honigpollenspezialisten stattgefunden. Sollten Pollenmonographien künftig nicht den ganzen Pollen (Exine, Intine und Zellinhalt) berücksichtigen, um nach verschiedenen Richtungen verwendbar zu sein?

E. VIEITEZ (Pontevedra)

El polen en las mieles de Galicia

Paper available in typescript.

SESSION 2

July 10th, 1.30—5.30 p. m., Attendance: 50 members

Chairmen: H. GODWIN and H. HYDE, Recorders: G. ERDTMAN and O. HEDBERG

SUBJECT:

Aerobiological and Technical Aspects of Palynology, Pollen Analysis (Quaternary Deposits)

Demonstration of Soil Sampler and Peat Augers

Two peat augers (Hiller model) by BEUS and MATTSON, Mora, Sweden, were demonstrated at Stora Mossen. Augers of the larger model (rods 1.5 m, container 0.5 m) would generally be preferred to those of the smaller model (rods 1 m, container 0.3 m). An auger of the latter type can be easily handled by a single person.

At the same time the Royal Swedish Geotechnical Institute demonstrated a soil sampler with metal foils, a new device for taking undisturbed samples of very great length. This has been described by W. KJELLMAN, T. KALLSTENIUS, and O. WAGER (Proc. Roy. Swed. Geotechn. Inst., No. 1, Stockholm 1950). The leading principle of the new sampler is the complete elimination of the sliding resistance between the sample ("the core") and the inside of the sampler. This is achieved by insulating the core from the inside of the sampler by means of a number of thin axial metal strips of foils. Their upper ends are attached to a piston placed in the sampler immediately above the core. The

piston, which is not tight-fitting, is attached by means of a chain or a rod to a driving scaffold on the soil surface. Thus, the piston, together with the upper ends of the foils, is kept on a constant level while the sampler is driven down. During the driving, the inside of the sampler slides against the foils. The resulting friction causes a pulling force in the foils and their anchorage, but does not affect the core. There is no sliding between the core and the foils. The inner diameter of the sampler tube is 68 mm. As the sampler and the core enclosed therein are withdrawn, they can be divided into 2.5 m long sections. In soft soils pushing is the simplest way of driving the sampler down. This is done by a mechanical driving and withdrawal device. In harder soils there is usually some friction between the soil and the sampler and this is reduced by means of jets of water or special fluids applied outside the sampler, just above its cutting edge. In harder material, such as brown coal, a rotating outer tube with a toothed steel bit at its lower end is attached, and the drilling fluid is pumped down into the interspace between the sampler and the tube.

In order to make the sampler lighter and easier to transport and handle, a new model is now being designed. Its inner diameter will be 40 mm, and the number of foils will be reduced from 16 to 12. A new driving device will be designed, which will also be portable but lighter and handier than those used up to now. All these modifications will make it cheaper to take long cores in soft soils in the future.

At Stora Mossen cores of marsh peat, lacustrine ooze, and varved clay were obtained. Such cores consist of absolutely clean material suitable for the investigation of megafossils as well as microfossils. Baroness EBBA HULT DE GEER gave a special demonstration of the varved clay and the geochronological methods of Professor GERARD DE GEER.

H. HYDE (Cardiff)

Atmospheric Pollen Studies in Great Britain in their Relation to the Pollen Analysis of Post-Glacial Deposits

The incidence of atmospheric pollen in Great Britain has been studied by the "gravity" slide method from late 1941 onwards. The annual catch at various places and in different years varied between 1100 and 6800 grains on 1 sq. cm.

Pollen productivity varies significantly from year to year in almost all types. In certain trees high annual catches are or appear to be repeated at the yearly intervals stated: *Quercus* (5), *Pinus* (2), *Fagus* (2), *Fraxinus* (3) and *Ulmus* (3). The order of relative pollen productivity of the principal types of trees is as follows: 1. *Quercus*, 2. *Corylus*, 3. *Fraxinus*, 4. *Alnus*, 5. *Carpinus*, 6. *Fagus*, 7. *Pinus*, 8. *Betula*, 9. *Ulmus*, 10. *Tilia*.

In Wales and probably throughout Great Britain, apart from large towns, it is possible to distinguish between two altitudinal zones, viz. 1, lowland, up to about 1250 ft (375 m), highly productive of pollen, giving high catches, the catch at a given point being very largely local; and 2, upland, above about 1250 ft, almost non-productive, giving in general relatively low

catches, the catch at a given point being almost all of lowland origin. The average tree spectra from two stations situated well inside the upland zone have been worked out and compared with the areas from which certain groups of pollen were presumed to have been derived. The results showed wide discrepancies between the proportion of tree pollen to total pollen catch and that of woodlands to the total area, between that of grass pollen to total catch and that of lowland grassland to total area and so on.

The relation between non-tree and tree pollen at stations situated in lowland areas, as was to be expected, was found to be closely related to production on or near the site of the apparatus.

The principal tree pollens which have been recognised in the pollen analysis of English and Welsh peats and sediments all (except *Carpinus*) come high in the list of pollens arranged in overall order of aggregate catches (all stations taken together). *Fraxinus*, *Sambucus* and *Acer* also stand high, as in town analyses do planted trees of various kinds. Grasses stand much higher in relation to the total of non-tree pollens than is usual in fossil counts, though the cereal fraction is low. By comparison with fossil counts the proportion of each of the other non-tree pollens in relation to the total of such pollens is in general also low at all stations.

Discussion

H. GODWIN: Could the variation in flowering demonstrated in *Ulmus* be due to early spring frosts?

H. HYDE: Yes, probably.

J. IYERSEN: In a post-glacial sample from Greenland I once found a pollen grain of *Castanea* which implies a long distance transport of 3,000 km or more.

G. ERDTMAN: During two years (June 1947-1949) the absolute number of pollen grains sinking through the sea water at Bornö near Gothenburg has been calculated by means of a special apparatus exposed 15 m below sea level. The total number collected per square metre of exposed surface was approximately 80 million per year (80 per sq. mm and year). Investiga-

tions of pollen grains in sediments laid down at considerable distance from pollen-producing vegetation may provide information about the history of the latter: thus many pollen grains were found in deep sea sediments in the Mediterranean between Naples and Sardinia (C. LARSSON: Examination of Pollen Grains in Three Cores from the Tyrrhenian Sea. With an Appendix by G. ERDTMAN.—Meddel. Oceanogr. Inst. Göteborg 15.—1948).

K. FAEGRI: In response to Dr. ERDTMAN's suggestion that oceanic sediments should be utilised for the study of terrestrial vegetation, I wish to point out that the deep-sea cores so far studied have, as a rule, proved devoid of pollen grains.

N. POLUNIN (Montreal)

Pollen in the Air at High Latitudes

I live chiefly in a far-off land in which such flying and other facilities as I require for some of my work are only obtained through governmental agency. For this one has to pay by submitting one's results. In other words, papers have to be "cleared" before publication. Now it is with the greatest regret that I have to announce that the paper and illustrations which I had laboured so happily and so long to prepare for presentation to you today has not been so cleared. It was submitted already weeks ago and when some days back the position still remained doubtful both Professor Skottsberg, our Congress President, and my Diplomatic friends tried to get the necessary permission for me at least to speak about my methods and observations; but all in vain, the news came during the weekend that I must not give this and another paper, or discuss the material involved. I trust you will understand, Ladies and Gentlemen, and accept this expression of my sincere regret and keen personal disappointment.

K. FAEGRI (Bergen)

On the Presentation of Pollen-Analytical Data

The results of a pollen-analytical investigation are generally presented as a diagram. As

pollen diagrams are a practical aid, they should be as strictly standardised as possible to facilitate the reading. They should also contain a maximum of information without being crowded, and it is essential that the statistical validity of conclusions can be checked. Different problems demand different diagram types, and it will not serve science to lay down too strict rules. On the other hand pollen analysts should exercise self-control with regard to innovations that are not absolutely necessary for the elucidation of the problems under consideration. Certain basic rules should always be kept in mind, e.g. the binding together of all data pertaining to one sample by means of a horizontal line, the introduction of lines that permits the reader to find out the percentage values directly from the diagram, etc.

F. FLORSCHÜTZ (Velp)

On the Palynological Boundary Pliocene-Pleistocene in Europe

In the Netherlands the "clay of Reuver" (Reuverian) is generally considered as the youngest terrestrial Pliocene formation. It contains a great deal of macroscopic remains of plants, among which are particularly conspicuous the genera *Actinidia*, *Carya*, *Cinnamomum*, *Epipremnum*, *Eucommia*, *Euryale*, *Fagus*, *Liquidambar*, *Liriodendron*, *Magnolia*, *Nyssa*, *Phellodendron*, *Pseudolarix*, *Pterocarya*, *Sesquoidia*, *Stuartia*, and *Zelkova*.

The Pleistocene period began with a deterioration of the climate manifesting itself especially in the Foraminifera and the marine Mollusca. The flora of this Praetiglian is little known. The superposed Tiglian, on the contrary, perhaps an interstadial of the early glaciation, contains in the "clay of Tegelen" the remnants of a rich plant community. It greatly differs from that of the Reuverian but still includes some "Tertiary" elements, such as *Actinidia*, *Eucommia*, *Euryale*, *Magnolia*, *Phellodendron*, and *Pterocarya*. Among the "meso-fossils" *Azolla tegeliensis* is typical. Dutch palaeo-zoologists regard the Tiglian mammalian

fauna with e.g. *Archidiskodon meridionalis*, *Equus robustus*, *Leptobos* cf. *elatus*, *Macaca florentina* and *Trogontherium boissiletti*, and the Villafranchian from Italy and France as synchronous.

Palynological investigations accentuated the difference between the Dutch Upper Pliocene and Lower Pleistocene, thus sharpening the botanical boundary Tertiary-Quaternary in the Netherlands. The Reuverian is characterized by an association of pollen grains i.a. of *Fagus*, *Liquidambar*, *Nyssa*, cf. *Taxodium*, *Sciadopitys*, and *Sequoia* or *Cryptomeria*; the Tiglian by a group including pollen grains of *Carya*, *Phellodendron*, *Pterocarya*, and *Tsuga*, also occurring in the Reuverian.

An analogous dissimilarity appears to exist in Italy where in Pliocene layers in the Arno Valley (Castelnuovo dei Sabbioni) and the Serchio Valley (Garfagnana) pollen grains of *Nyssa*, cf. *Taxodium*, *Sciadopitys* or *Cryptomeria* have been found, whereas Villafranchian deposits in the Sieve Valley (Mugello) and the neighbourhood of Lefte (Lombardy) produced pollen of *Carya*, *Pterocarya* and *Tsuga*.

The preliminary conclusion seems justified that during the transition Pliocene-Pleistocene the composition of the forests in various parts of Europe suffered an essential and nearly similar modification.

H. T. WATERBOLK (Groningen) *Palynological Investigation of Burial Mounds*

The paper deals with the preliminary results of an investigation of fossil surface samples. These can be obtained from fossil soil profiles e.g. below prehistoric burial mounds. Especially when the barrows have been erected on a vegetation with a profile containing much raw humus, such as the Calluneto-Genistetum, the pollen content is unexpectedly high and its preservation is fairly good. By analyzing these samples we get fossil surface spectra, which can be used to form an idea of the vegetation at the time when the barrows were constructed, and

which for the purpose of dating can be compared with pollen diagrams from peat bogs in the area concerned.

Analyses have so far been made of samples from a great number of barrows from different parts of the Netherlands. The age varies from Neolithic to Iron Age.

The most important phenomenon in the vegetation development of the Subboreal period is the expansion of *Calluna*, which according to many investigations took place at the beginning of the Bronze Age. It now appears from my analyses that during the construction of the oldest Neolithic barrows the heaths had not yet been formed. From below late Neolithic barrows, at least when they were lying in the same region as the former ones, values up to 100 % were found. In such regions, however, where occupation started later on, for example during the middle Bronze Age, low *Calluna* values may be found as late as that period. Apparently the appearance of the heaths is an attendant phenomenon of man's interference with his surroundings and its date may vary from place to place. Nevertheless, the podzol profile never occurs until the beginning of the Bronze Age. This indicates a climatic change at this time, stimulating the podzolization and also in this way favouring the heather.

Another result of the barrow examinations concerns *Tilia*. In Neolithic times it is present throughout the country, sometimes with values up to 40 %. During the Bronze Age, however, the tree disappears from the northern part of the country, whereas in the middle and southern regions values up to 20 % are still to be found. In the early Iron Age *Tilia* disappeared from the whole country. No definite explanation of this phenomenon can as yet be given.

The values of *Fagus* show strong local variation, which can be explained by the facts that *Fagus* requires good soils and that its pollen is not easily transported over long distances.

Discussion

H. HYDE: GODWIN in England and others both in that country and elsewhere have established

correlations between human cultural periods and pollen-analytical zones by the examination of finds made in peat bogs. More recently peaty material from beneath a Welsh megalithic monument has been pollen-analysed and its pollen content compared with that of a neighbouring bog. Dr. WATERBOLK's paper points the way to establishing such correlations even at the absence of peat or lake sediments and it is to be hoped that this method may be applied to the investigation of tumuli elsewhere than in Holland: those of England and Wales offer a promising field of enquiry.

P. A. SEARS (Oberlin, Ohio)
Palynology in North America

The paper, which was read by Dr. GODWIN, has been published in *Svensk Botanisk Tidskrift* 45 (1951), p. 241-246.

E. M. VAN ZINDEREN BAKKER
(Bloemfontein)
Palynology in South Africa

Published in *Svensk Botanisk Tidskrift* 45 (1951), p. 254-256.

SESSION 3

July 11th, 9 a. m. — noon, Attendance: 70 members

Chairman: R. POTONIÉ, Recorders: G. ERDTMAN and O. HEDBERG

SUBJECT:

Prequaternary Pollen Grains and Spores

Demonstration of the Palynological Laboratory

G. ERDTMAN demonstrated the Palynological Laboratory, the collections of pollen and spore slides, the palynological archive containing descriptions of about 10 000 slides and excerpts from literature on pollen morphology and plant systematics, etc. Among the slides exhibited were slides of Early Jurassic spores and pollen grains, e.g. *Tricolpites troedssonii*. This pollen is of special interest as grains of this type have so far only been encountered in dicotyledonous plants. Electron microscope photographs and drawings for a text-book on pollen morphology and plant taxonomy were exhibited. Also on display were 20 wall charts illustrating the palynological terminology (polarity, sporoderm stratification, apertures etc.) adopted in the laboratory. This terminology has been described in a manuscript which was sent to Lucknow in November 1949 for printing. It differs in certain respects from that of FÄBRI

and IVERSEN but the interpretation of palynological features is similar.

O. WETZEL (Eutin, Holstein)
Die Mikropaläontologie des baltischen Kreide-Feuersteins

Published in *Svensk Botanisk Tidskrift* 1951, p. 249-253.

Discussion

P. THOMSON: A. EISENACK hat in einigen Publikationen als Hystrichosphaerideen Formen mit deutlicher Tetradenmarke abgebildet. Die Geschiebe aus denen sie stammen sind in Ostpreussen gefunden worden und dürften einwandfrei aus dem Devon stammen. Im anstehenden Silur und Ordovizium in Estland habe ich nie Sporen mit Tetradenmarken beobachtet. Wir haben uns in dieser Angelegenheit mit A. EISENACK geeinigt.

R. POTONIÉ and G. ERDTMAN expressed the

opinion that palynologists should devote attention not only to pollen grains and spores but also to other microfossils.

ELISE HOFMANN (Wien)

Pollenkörner im Oberkreideflysch von Muntigl bei Salzburg

Eine Zone von Sandsteinen und mergeligen Schiefern bildet in verschiedener Breite den Aussenrand des Alpen-Karpathen-Bogens. Dieses als Flysch bezeichnete Gestein, den Kalkalpen im Norden in ihrem ganzen Verlauf vorgelagert, gliedert sich nach heutigen Erkenntnissen in einen der Oberkreide und einen dem Eozän angehörigen Anteil. Zum Oberkreideflysch zählen Sandsteine und Mergel mit reichlichen, als „Fukoiden“ bezeichneten Resten, teils pflanzlicher Natur, teils Kriechspuren und Bohrgänge verschiedener kleiner Würmer. Der Muntigler Flysch gehört der Oberkreide an, ist hellgrau, sehr feinkörnig und ohne sichtbare gröbere pflanzliche Einschlüsse. Es erwies sich relativ reich an Pollen: hauptsächlich findet sich Dreieckspollen, darunter solcher mit je einer Pore an den Ecken, an denen die Exine etwas verdickt erscheint. Die Grösse des Kornes beträgt etwa 30 μ . Der intensive Vergleich dieses Pollens mit dem verschiedener *Nyssa*-Arten, ferner mit Arten von *Eucalyptus*, *Engelhardtia* und *Betula* ergab keine Übereinstimmung mit dem fossilen Pollen, auch nicht der Vergleich mit Abbildungen aus der Literatur. Hingegen zeigt rezente *Rhizophora mucronata* typischen Dreieckspollen mit ziemlich dickwandiger Exine, deutlich sichtbaren Poren und einem kreisförmigen Innenareal. Die Poren haben einlippige Wände und erscheinen etwas keulenförmig verdickt. Durch Deformation des rezenten Pollens, hervorgerufen durch Liegen in Glycerin, Behandeln mit konz. Schwefelsäure oder Kochen in Kalilauge entstehen dem fossilen Pollen überaus ähnliche Formen. Das Endprodukt der Fossilisation ähnelt dem Endprodukt der Deformation rezenten Pollen. Es finden sich sowohl bei dem fossilen als auch bei

dem rezenten Pollen von *Rhizophora mucronata* die gleichen Stadien der Deformation. Nach meinen Studien kann das Vorkommen von Pollen nach dem Typus *Rhizophora mucronata* im Flysch von Muntigl demnach als gesichert angesehen werden. *Rhizophora mucronata* ist eine Pflanze der Mangrove an den Küsten des Indischen Ozeans von Afrika bis Australien.

Auch die in der amerikanischen Mangrove auftretende Art *Rhizophora Mangle* konnte ich nach Vergleich mit rezentem Pollen dieser Art fossil in Muntigl nachweisen. Bei ihr bildet der Pollen Pakete oder Massulae von ovaler Gestalt, welche ich auch fossil auffinden konnte. Auch Massulae vom Typus *Xylocarpus moluccensis* fanden sich im Flysch von Muntigl. Diese Pflanze lebt heute in der Mangrove der Alten Welt. Unter dem fossilen Pollen von Muntigl fanden sich ferner auch Dreifaltpollen, die dem Typus *Avicennia nitida* eingereiht werden können, gleichfalls einem Element des Mangrovetwaldes der Alten und Neuen Welt. Ausser diesem Pollen von Mangrovearten konnte ich im Flysch von Muntigl auch noch solchen vom Typus *Pterocarya*, *Nymphaea alba* und Körner vom Typus *Pinus silvestris* und *Pinus haploxyylon* feststellen. Zwei Formen von Pollen fand ich im Muntigler Flysch auf, ebenfalls Dreieckspollen, der aber mit rezentem Pollen nicht identifizierbar war. Ich habe diese beiden Arten zur Evidenzhaltung dieses Vorkommens als *Pollenites salisburgensis* n. sp. und *Pollenites Abelii* n. sp. benannt.

In den Flyschproben finden sich auch Reste von Oberhäuten, z. B. rosettig gelagerte dickwandige Zellen einer Blattoberseite, welche mit der Epidermis von *Rhizophora mucronata* übereinstimmen, ferner solche, die mit der Oberhaut von *Platyserium* sp. sehr gut in Einklang gebracht werden können.

Von Sporen sind im Muntigler Flysch solche vom Typus der *Lycopodium*-Arten und solche eines *Platyseriums* vertreten, welches heute epiphytisch lebend in der Mangrove vorkommt.

So gibt der Flysch von Muntigl durch seine zahlreichen pflanzlichen Mikrofossilien, wie Pollen, Sporen und Gewebsreste von Typus wich-

tiger Mangrovepflanzen den Beweis, dass er als eine fossile Mangrove gedeutet werden kann, eine Vermutung, die O. ABEL nach seinen Studien an der amerikanischen Mangrove geäußert hat und die nun durch die Pollen-, Sporen- und Kutikularanalyse bestätigt wird.

Discussion

R. POTONIÉ asked Prof. HOFMANN to publish an account of the methods used in isolating the pollen grains.

P. THOMSON (Liblar b. Köln)

Aufbereitung von Sporomorphen in Braun- und Steinkohlen

Das ideale Aufbereitungsmittel für Braunkohlen und schwach eingekohlte Steinkohlen ist H_2O_2 . Man erwärmt ca. 1 g zerkleinerter Braunkohle mit der 20-fachen Menge von 10 % H_2O_2 auf einer Kochplatte 10–15 Minuten. Dann wird die Probe ausgewaschen und zentrifugiert und mit verdünnter Lauge (NaOH oder KOH) unter 10 % aufgekocht. Nach erneutem Auswaschen werden Glycerinpräparate hergestellt. Bei Steinkohlen dauert der Bearbeitung mit 10 % H_2O_2 1–4 Stunden. Der Vorteil dieser Methode, die der Verf. mit N. REIN ausgearbeitet hat, ist dass sich keine giftigen Gase bilden und dass man keinen Abzug benötigt.

Discussion

J. DIJKSTRA: Is it possible to determine to which part of the Tertiary a certain brown-coal belongs, even if there are only a few samples at hand?

P. THOMSON: This is possible in most cases; but, of course, the greater the number of samples the greater is the accuracy.

R. POTONIÉ: Even unidentified pollen grains and spores can profitably be used as guide fossils.

F. FIRBAS had found H_2O_2 useful in the preparation of Interglacial material.

ELIZABETH KNOX (Edinburgh)

Spore Morphology in the Lycopodiales and its Significance in the Study of Palaeozoic Microfossils

A morphological study of the microspores of the living genera of *Lycopodiales* has made possible an arrangement of the species in groups characterized by the possession of similar exospore ornamentation. In the genus *Lycopodium* four groups are recognised; in three of the groups the spore sculpturing is pitted and in the fourth the ornamentation is reticulate. In the genus *Selaginella* the microspores are divisible into two main series, (1) those with a membranous outgrowth, either encircling the spore entirely or reduced to an annular ring, and (2) those furnished with outgrowths or protuberances from the wall, e.g. spines, tubercles, rod-like processes etc., variable in size, shape and disposition. In *Selaginella* twenty groups have been differentiated.

On the basis of the same criteria, suggestions are advanced for an arrangement of Palaeozoic spores into form genera. A classification of fossil microspores is put forward based upon the "Annotated Synopsis of Palaeozoic Spores" of SCHOPF, WILSON and BENTALL (1943). Four new genera are proposed, making a total of 17 genera of fossil microspores.

Close parallels between the microfossils and spores of living genera are cited and possible affinities with Bryophyta are suggested.

Discussion

P. THOMSON: Dr. KREMP hat feststellen können, dass einige Mikrosporen wie *Densospora* u. a. immer in Mattkohlen, die arm an Vitrit sind, auftreten, wie der cf. Cupuliferen-Pollen in den „hellen Schichten“ der Braunkohlen in N. W. Deutschland. Dürfte ich Sie fragen, ob das auch im Karbon in England der Fall ist?

G. ERDTMAN: The results of these painstaking and detailed investigations are of great value to the palynologists. It would be interesting to have supplementary knowledge of the sporo-

derm stratification. To attain this it would probably suffice to study one or a few representatives of each morphological group distinguished by Mrs. KNOX.

J. HSÜ (Lucknow)

Devonian Spores from Yunnan, China

Ninety-two forms of spores and spore-like bodies have been obtained from the Lower and Middle Devonian rocks of Central Yunnan, China.

From the region of Poshi in the district of Hwaling 57 spore-like forms have been discovered. Of these, 51 forms are pteridophyte spores whereas 6 forms are described as "spore-like bodies". Twenty-seven of them are alete, 21 types possess a triradiate mark, and the remaining three have one or three elongate furrows. The trilete spores are usually large, ranging from 20–100 μ in diameter, while the alete ones are generally smaller. Most of the spores are spherical or ellipsoidal and possess different kinds of wall sculpturing. While the great majority of spores are unicellular, three of the alete spores are multicellular. Two spores are assumed to be comparable with those of *Psilophyton princeps* and *Protopteridium minutum*, and one of them recalls "Spore-type H" of LANG. Still another type seems to have belonged to an *Asteroxylon*-like plant. The affinities of the others are difficult to judge as little is known to date about spores from Devonian deposits.

From Tatsun in the district of Lunan 34 forms of spores and one type of a spore-like body have been obtained. Most of them possess a triradiate mark. Four of these appear to be megaspores of lycopods, three are probably isospores of lycopods, one type of spore has possibly Calamarian affinity and the remainder are probably microspores or isospores of other groups of pteridophytes.

F. LONA (Milano)

Pollenanalytische Untersuchungen in der Po-Ebene

Es wurden die Ablagerungen zweier Seen in der Po-Ebene pollenanalytisch untersucht; die Lage des einen bei den Monti Berici ist ca. 40 km südlich des Randes der alpinen Würm-Moränen, die des anderen bei den Eugadischen Hügeln ca. 70 km südlich derselben Moränen.

Die Untersuchung lieferte Diagramme, welche von der Gegenwart sehr weit zurückziehen, wahrscheinlich bis in das späteste Würm-Maximum. Die Ergebnisse erlauben es daher, sich ein Bild der Vegetation der Po-Ebene auch während der Glazialzeit zu machen. Die Profile (eines davon erreicht eine Tiefe von 15,50 m) lassen sich in zwei grosse Abschnitte teilen: a) ein älterer Abschnitt mit *Pinus* und *Salix*, alternativ herrschend, wobei ein mehr oder minder hoher Prozentsatz von *Betula* beigelegt ist und sporadisch auch *Picea* (ausserdem manchmal auch *Alnus*); b) ein jüngerer Abschnitt mit vollständiger Bewaldung (*Quercus*, *Ulmus*, *Tilia*, *Castanea*, *Fagus*, *Abies*, *Corylus*, *Alnus*). Der Übergang zwischen diesen beiden Abschnitten, d. h. die gewöhnliche Kiefern-Periode mit Spuren von Thermophilen, ist in den verschiedenen Diagrammen mehr oder minder ersichtlich.

Das bisherige Ergebnis zeigt mit Bestimmtheit, dass während der letzten glazialen Zeit im Nordosten der Po-Ebene wenigstens kleine Areale vorhanden waren, welche von subarktischer tundraähnlicher Vegetation mit vorherrschender *Salix* und wenig *Pinus* mit verhältnismässig reicher Grasbedeckung bestanden waren, während andere Bäume selten waren.

Discussion

F. FLORSCHÜTZ, F. FIRBAS, and G. ERDTMAN: Were any megafossils or *Artemisia* pollen grains found?

F. LONA: No such fossils were found.

SESSION 4

July 11th, 1.45—5.00 p. m., Attendance: 40 members

Chairman: F. FIRBAS, Recorders: G. ERDTMAN and O. HEDBERG

SUBJECT:

Position and Needs of Palynology, Nomenclature

The Chairman, in opening the session, proposed that the Conference should forward to the Swedish authorities a resolution emphasizing the desirability of maintaining the Palynological Laboratory at Bromma as a permanent research centre. The resolution, written in German and English, was adopted. The German version is as follows:

„Im Rahmen des 7. Internat. Botaniker-Kongresses in Stockholm 1950 haben Wissenschaftler aus 21 Ländern und aus allen Erdteilen im Palynologischen Laboratorium in Bromma eine Konferenz abgehalten, zahlreiche Vorträge gehalten und anregende Diskussionen geführt. Sie haben dabei neuerlich die grundlegenden Arbeiten kennen und achten gelernt, die Dr. G. ERDTMAN seit vielen Jahren geleistet hat und die für alle ganz unentbehrlich sind—gleichgültig ob sich das spezielle Interesse des einzelnen mehr auf die Probleme der botanischen Systematik und Phylogenie, der Paläobotanik, der Geologie des Quartärs, des Tertiärs oder älterer Formationen, auf solche der Archäologie und Siedlungsgeographie, der Klimatologie und Meteorologie, auf Fragen der Medizin (Pollenallergie) oder der angewandten Botanik (Nahrungsmitteluntersuchung) richtet. Die Vertreter aller dieser wissenschaftlichen Disziplinen begrüßen es auf das lebhafteste, dass Schweden, das Land Linnés, ein Institut besitzt, das durch den Umfang seiner Vergleichssammlungen von Pollen und Sporen und durch deren gründliche Bearbeitung in der Welt nicht seinesgleichen hat und das ihnen durch die hier gesammelten Erfahrungen eine sehr grosse Hilfe sein kann. Sie haben mit Bedauern gehört, dass das Palynologische Laboratorium bisher nur

eine provisorische Einrichtung ist, und dass es daher fraglich ist, ob sich Dr. ERDTMAN dieser Aufgabe wird dauernd widmen können. Sie erlauben sich daher an die zuständigen staatlichen Stellen Schwedens die Bitte zu richten, die Existenz dieses Instituts auf die Dauer zu sichern.“

G. ERDTMAN, in expressing his gratitude, hoped that the enthusiastic passing of the resolution was indicative of the importance of palynological studies and also of the growing interest taken in this branch of science throughout the world.

He also took the opportunity of requesting a quick interchange of reprints. This is, e.g., necessary to make the annual lists of literature on palynology as exhaustive and efficient as possible.

R. POTONIÉ (Düsseldorf)

Über die Nomenklatur der tertiären und älteren Pollenkörner und Sporen

Von 1931 ab habe ich gemeinsam mit meinen Schülern (GELLETTICH, İBRAHİM, LOOSE, THIERGART, VENITZ, WICHER, WOLFF usw.) begonnen, tertiäre und ältere Pollenkörner und Sporen, soweit sie nicht einwandfrei zu rezenten Arten gestellt werden konnten, als Formspezies und Formgenera aufzufassen. Wir haben dementsprechende Namen eingeführt. Es wird vorgeschlagen, diese weiter so zu handhaben und sich dabei nach den Internationalen Nomenklaturregeln zu richten.

Wenn wir in der Lage waren, Pollenkörner oder Sporen zu einer natürlichen Gattung zu stellen, so gaben wir dies an durch Bezeich-

nungen wie *Ilex-pollenites iliacus* und *Ilex-pollenites margaritatus*.

War die Beziehung zur Gattung nur formal gegeben, so schrieben wir z. B. statt *Sabal Sabaloidites areolatus* (vielleicht auch *Sabaloid-pollenites*).

Konnte die Verwandtschaft nur auf die Familie bezogen werden, so wurde ein Ausdruck wie *Polypodiaceae-sporites haardti* gewählt usw.

Liess sich die Form gar nicht oder nur schlecht bei rezenten Gattungen oder Familien einreihen, so wurde ein neuer Formgattungs-Name geschaffen, der sich nur auf die Gestalt und gar nicht auf das System der natürlichen Pflanzenfamilie bezog.

Ein neuer Name für die Formspezies wurde in allen Fällen für nötig gehalten, wo sich die fossile Form nicht einwandfrei mit einer einzigen rezenten Art identifizieren liess.

Es wird vorgeschlagen, dies in ähnlichem Sinne weiterhin so zu handhaben.

Es steht damit eine angenähert natürliche Klassifikation neben einer rein auf Gestaltsgruppen eingestellten. Das angenähert natürliche System soll die fossilen Sporomorphen soweit wie möglich an die natürlichen Familien, Gattungen, Sektionen und Arten heranbringen.

Es sei hier auf die Arbeit von R. POTONTÉ, P. THOMSON und FR. THIERGART, Zur Nomenklatur und Klassifikation etc. (Geol. Jahrb. 65, S. 35-70, Hannover/Celle, 1950), verwiesen, wo diese Methode der Nomenklatur und Klassifikation an Hand der neogenen Sporomorphen praktisch durchgeführt worden ist. Weiter sei die Dissertation meines Schülers IBRAHIM von 1933 an der Technischen Hochschule, Berlin, genannt, wo meine Klassifikation carbonischer Sporen angewandt wurde.

R. A. COUPER and W. F. HARRIS (Wellington), ISABEL C. COOKSON and SUZANNE L. DUIGAN (Melbourne)

Terminology and Nomenclature for Fossil Pollens and Spores

Six recommendations for the nomenclature of fossil pollens and spores are put forward.

Each recommendation is illustrated by examples of the suggested nomenclature using fossil pollens and spores found in Jurassic, Cretaceous and Pliocene-Pleistocene carbonaceous deposits in New Zealand.

The principles underlying these recommendations are:

1) A name should always be associated with a type.

2) Whenever the pollen or spore form indicates affinity with a living species, genus or family the specific, generic or family name should be included in the binomial nomenclature.

3) The International Rules for Botanical Nomenclature should be strictly observed.

4) When new genera (i.e. form genera) are created for pollen or spore forms, their systematic position in relation to plant categories of higher rank should be indicated as far as possible.

The terms "sporomorph" and "id" were also briefly commented on.

Discussion

Contributions were made by Miss MOORE and Messrs ERDTMAN, FAEGRI, GODWIN, JONKER, MITCHELL, POTONTÉ, SCHOFF, and SELLING. Six recommendations for the nomenclature of fossil pollen grains and spores put forward by COUPER, HARRIS, COOKSON and DUIGAN were read by Miss MOORE and extensively commented upon. The term "sporomorph" should not be used in a taxonomical sense but only as a morphological term (a comprehensive designation of pollen grains and spores). The following resolution—a recommendation for students of plant microfossils and for palynologists in general—was adopted:

1. Whenever formal taxonomic classification of fossil and subfossil pollen grains and spores is desirable or necessary, palynologists should regard them as representative of form genera or form species in the sense of taxa according to the International Rules of Botanical Nomen-

clature. Nomenclatural types should be designated wherever the Rules require it.

2. In cases of uncertain identification it is often preferable to propose new artificial taxa rather than to apply old names in a loose or inexact sense conducive to confusion.

3. If pollen grains and spores show characters restricted to one species of the modern flora, identifications should be made with the modern species and genus.

4. It is desirable to describe and illustrate spores or pollen grains of the living species whenever fossil spores or pollen grains are first identified with it. If the modern forms are already described and illustrated, references should be given.

5. If pollen grain or spore characters are not restricted to a single modern species, identification with a modern species is always to be avoided.

6. If pollen grain and spore characters are restricted to a group of species included in a modern genus, the name of the subgeneric group or other indication of the group of species should be given (e.g. *Coprosma*, aff. *C. propinqua*-group).

7. If pollen grain or spore characters are similar within a modern genus, fossil spores or pollen grains may be identified with the genus, but an inclusive form may need to be established.

8. If the above procedures are not applicable, fossil pollen grains or spores may be used as a basis for establishing new form genera in accordance with the Rules.

9. If form genera are resorted to, an author should indicate the smallest taxonomic subdivision of the plant kingdom to which they can be consistently referred.

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